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QUANTITATIVE RELATIONSHIP BETWEEN STIMULUS
AND EFFECT IN THE STATIC ORGAN

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QUANTITATIVE RELATIONSHIP BETWEEN STIMULUS AND
EFFECT IN THE STATIC ORGAN

THESIS

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by

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INTRODUCTION

The experiments described in this thesis can be summarized under one heading: research into the quantitative relationship between stimulus and effect in the static organ.

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One will not find any new argumentation for the Mach-Breuer theory. We are convinced that this theory is correct in principle. To prove this, a brief summary of the historical literature will precede the experiments; in addition, there is a review of the theory in which the weaker points of the explanation are brought forward.

The experiments are divided into two principle sections:

1. Experiments on the otoliths;
2. Experiments on the semicircular canals.

The acceleration stimulus in all of these was as uniform as possible and its effect was determined by recording the reflexes or determining the threshold of the sensations.

The technical difficulties with the progressive movements, necessary for the otolith organs forced us to work with animals only for the time being. Here, too, uniform acceleration was employed. In the guinea pig, we studied the reflex time at different degrees of acceleration, including the minimum energy which would still evoke a reflex.

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The second section includes two main groups: reflexes in animals, and sensations and reflexes in man.

The animals used are the pike, frog, turtle and guinea pig.

In the frog, which is by far the most suitable from the above standpoints, we analyzed the head movement during rotation in the horizontal plane; in particular, we examined the ratio between the intensity of the stimulus and the liveliness of the movements, such as those considered as sensations in the law of Weber.

In the case of the turtle and guinea pig, we had to restrict ourselves for technical reasons to measuring the reflex time during rotation, and in the case of the pike, to the reflex time for the eye nystagmus with an electrical stimulus of known strength.

For man, we gave the most attention to the sensations and determined successfully the quantitative prerequisites, which include the following:

1. The minimum sensation, taking into account the minimum energy employed.
2. The minimum distinction in sensation.
3. The merging of sensations.
4. We attempted to construct a curve describing the force of an after-sensation.

With respect to reflexes in man, we measured the reflex time of the rotation nystagmus.

Finally, we have directed some general remarks to the question of whether some additional peculiar traits are to be found in the expression of hearing and the static senses which indicate their anatomical relationship.

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This chapter is of more general significance, as we did not perform special experiments but rather looked at daily life for the answers to this question.

CHAPTER I

LITERATURE SURVEY

As early as 1897, Ch. Koning (in his dissertation [42] on the semicircular canals) began his historic summary with the statement that a somewhat complete report of the experiments performed until then in the field of the non-acoustic function of the ear would take several years of continuous work. At present, the amount of work has doubled as we see in the surveys of S. von Stein [67,68] and A. Kreidl [44].

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We must confine ourselves to a brief summary of the most important facts related to the subject and who discovered them, as well as the theories under which they fall. The numerous repetitions of experiments by several researchers will remain outside the discussion.

First let us deal with the sensations, and then with the reflexes stimulated by the labyrinth.

§1. STATIC SENSATIONS

These sensations do not have a strong effect on our consciousness; hence, the part they play in the structure of our psyche has been underestimated or actually gone unnoticed for a long time. Only the abnormally strong sensations, summarized under the name of dizziness, have been studied since ancient times. Darwin in 1795, Autenrieth in 1802, and Brown-Séquard in 1853 went deeply into explanations concerning dizziness after rotation and the reflexes that accompany it, such as vomiting, unconsciousness, and so on. Ritter found in 1803 that such dizziness could also be evoked by a galvanic current, conducted through the head. He assumed that stimulation of the brain was the cause. Purkyne [55], repeating the experiments of E. Darwin, analyzed carefully on himself the sensations following rotation and summarized his experiences in the following conclusions:

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- 1) The axis of the rotation sensation coincides with the axis

* Numbers in the margin indicate pagination in the original text.

of the head, even if the parallel axis of rotation lies outside;

2) By changing the position of the head during the after-sensation, the imaginary axis of the sensation appears to follow the head movement;

3) With slightly faster rotation, an illusion concerning the position of the vertical appears; that which leans to the outside (away from the axis of rotation) is observed as perpendicular, while one who is sitting or standing straight has the sensation of leaning to the outside and therefore feels compelled to lean towards the center, as strongly as is necessary to regain his balance.

That which is perpendicular, inside or outside all that is rotating, is seen as leaning.

To begin with, he concluded from 1 and 2 that an organ in the head had a part in this; he thought the brain most likely was involved because of its lesser consistency. Because of the passive change of position, this would change the cohesion of its particles somewhat and this would be felt.

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Menière found another localization of dizziness; he observed a similarity between the phenomena in the test animals of Flourens and an ear patient whom he treated, who died because of an acute infection which developed. Besides the reflexes, which were the same as those found by Flourens when he cut the semicircular canals, the patient had subjective dizziness and an increasing deafness. Menière, who was guided by these symptoms, during the autopsy examined the labyrinth and found a hemorrhage in the semicircular canals; the remainder of the inner ear was normal. Though he held to the acoustic theory of labyrinth function, and was thereby misled by the accompanying deafness, Meniere became the first to localize dizziness in the labyrinth.

A separation of sensory functions was first accepted by Goltz [33]. He repeated the experiments of Flourens and obtained the same results; with further experimentation, however, he came to understand better the nature of the reflexes and summarized these as aiding in balance. He supposed that head movements (involving the labyrinth and use of the senses) generated reflexes which regulated the position of the head and hence the position of the entire body, especially with respect to gravity.

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This last effect he supposed to be a stimulus. With a changed position of the head, gravity was assumed to create different pressure ratios inside the membranous labyrinth. A lower ampulla was assumed to experience a higher pressure of the endolymph on its inner wall than a higher one. The latter assumption had received sufficient physical opposition, but now attention had again been drawn to the experiments of Flourens and study of the labyrinth

ported again in many quarters.

The first one to publicize his observations, the physicist E. Mach, initially approached this subject along completely different lines, by means of an accidental observation of the illusion of Purkyne, the mechanism of which he (as a physicist) immediately explained as being a result of gravity and centrifugal force. Unfamiliar with the experiments of Purkyne, he investigated for himself to determine which physical laws applied to the passive movement of our body. He released a preliminary announcement in 1873 [49] with the conclusion: "On the basis of numerous experiments he had concluded that one could combine in one viewpoint the symptoms observed by Flourens and Goltz regarding orientation for balance and movement, dizziness, and eye movements, if one assumed that the nerves of the circular-canal ampullae of the labyrinth react with a rotational sensation to every stimulus (usually by means of a rotary momentum exerted on the contents of the circular canal)."

In 1875, he announced the details in his book [50], beginning with a summary of the physical laws, which must form the foundation of every inquiry into the observation of passive movements. He concluded from these laws the peculiarities on which these sensations must depend; at the same time, using his rotation apparatus, he convinced himself of the accuracy of his explanations. He has been reproached for this method of experimenting: because of his own premises, he suggested and found everything that he expected [76]. It was found later that even without being informed, every normal person has the same sensations if the circumstances are just as favorable as those which Mach chose. /8

Mach begins with the following laws:

I. Every acceleration of a body is caused by a change in the speed of another body and is a function of their masses.

In a free mass system the total of all forces is zero.

II. The center of gravity of such a system can be shifted only by external forces.

III. The law of the preservation of the boundaries. /9

IV. The principle of D'Alembert, which is derived from the preceding.

Mach constructed a rotation apparatus consisting of a large upright frame with a shaft through two horizontal posts; inside, a smaller frame was mounted, revolving inside the large one and parallel to its shafts. In the small frame, a chair revolved around a cross shaft inside and so permitted a subject seated on it to lean backwards more or less.

The whole apparatus was surrounded by a paper box, in order to exclude optical impressions.

He concluded from the above laws (and found confirmed) that:

1. Only accelerations are noticeable, because only then does a force act on the body. During rotation, centrifugal force is felt, but during slow rotation (i.e., 3° per second) it can be neglected. Since this one force acts on all organs, the heavier parts will trail behind the lighter ones (so far as movement is possible) and otherwise press on them; this can be felt.

In free fall, when the force is proportional to the mass and the acceleration is therefore equal in all parts, the mutual pressure of the organs will be zero.

2. The halting of a rotation will give the same impression as the starting, but opposite in direction. The force is then identical to that caused by rotation in the opposite direction. One cannot think of a way in which this can be distinguished without use of the eyes. Mutatis mutandis, the same is true for progressive movements in the three dimensions.

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3. If one turns uniformly, so that one does not sense anything, then the shifting of the axis of the body will cause a new sensation, which (by rotating 180° around an axis perpendicular to that of the rotation) will be twice as strong.

This he explains experimentally by sitting on the apparatus with a small freely rotating disc in his hand. At the start, the small disc is held back by inertia and so rotates in a direction opposite to that of the apparatus. If friction with its own axis causes it to stop, then it rotates just like the subject, around the axis of the apparatus; if it is turned 180° in its own plane, so that the bottom is on top, it continues to rotate because of inertia but now in the opposite direction (as seen from the top); its axis, however, keeps rotating in the same direction as the apparatus so that the disc now doubles its speed like the big frame with respect to its axis. For the body, this is equal to a doubled stimulus. In order to test this himself, the subject had to lie down on the frame and suddenly turn himself during one rotation from one side to the other. There are all stages in-between, and it was also found that changing of the head position alone has the same effect as changing that of the whole body.

4. If one turns faster, the resultant of the gravitation and centrifugal force becomes vertical and, by concentration of the acceleration toward the center, becomes one of the two movements from which one can analyze the rotation.

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This then is the already mentioned illusion of Purkyne. This

can be eliminated by leaning the head parallel to this resultant. Consequently, the body does not perceive the centrifugal force.

The progressive accelerations were less easy to purify, because in the past larger values had to be used on account of lower sensitivity so that one became aware of mild shocks. Mach ingeniously used his rotating apparatus for this also. First the small frame is fixed to the big one and rotates with it; then the outer one is stopped and the small one is detached and continues to rotate by inertia. Had one not sensed the first smooth rotation, then this manipulation would only show the change in progression for the sense-organ if we ignore the friction which slows down the second rotation. This is consequently felt as motion separate from the first motion.

He obtained pure progressive motions by using a small wagon, which could be pulled rapidly; vertical motions were indicated by a scale on one side of which the subject sat. This last motion is of course not perfectly vertical, because the motion of both pans of the scale, measured horizontally, brings them closer to the pivot of the scale.

Mach now discovered in the sensations, by taking everything into account, his physical laws, but still supplemented them by the following peculiarities:

I. For rotation:

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1. The sensation lasts often longer than the stimulus;
2. With continued stimulus, however, it ceases;
3. The sensitivity is high; minimum perceptibility is 2° to 3° acceleration per second;
4. No negative after-image shows up.
5. The sensations in opposite directions are positive and negative, so they can cancel one another out.

II. For progression:

The same laws hold, but all sensations are weaker and shorter, the after-sensations are less clear, the sensitivity is less (minimum perception for vertical movement is 12 centimeters per second) and this decreases still further because of adaptation of the sense-organ.

In both categories, the direction of the movement is correctly recognized.

III. The sensation of position, which shows up in the phenomena of Purkyne, remains outside the discussion.

He found, as Purkyne did, that an organ in the head detected these stimuli; this follows immediately from the fact that

during rotation, movement of the head alone is sufficient to cause one to feel the sensation, just as he showed for rotation of the whole body; he made a long series of experiments, with the purpose of excluding skin and muscle sensors, and all of these agreed with this opinion. Mach was of the opinion (contrary to Purkyne) that the labyrinth was the most likely organ because of its anatomic construction: this was because of the round canals, each in one plane and with liquid contents, likely to stay behind during rotation and to stimulate the crista ampullaris, and because of the experiments by Flourens, in which the same type of reflexes appeared as caused by the passive movements of man and animals.

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For progression, another organ must be involved, as this can have no effect on the semicircular canals. He found the sac-cule the most suitable, without giving any arguments.

Otherwise, Mach did not attach much value to the whole of the hypothesis, but emphasized that his physical explanation, with the directly corresponding sensations, will always remain the basis for every investigation in this field.

He changed his labyrinth hypothesis already in his "Bases", saying that no flow of the endolymph would occur (since the canals are too narrow) but only a change in the pressure on the crista ampullaris.

By calculating the energy involved, he tried to show that the strength of the stimulus was not less than that of light on the retina.

The observation of position means that we are faced with the problem that the organ must function continuously without becoming fatigued.

One week after Mach (in Nov. 1873) delivered his preliminary announcement to the Vienna Academy, J. Breuer, during a meeting of the Royal Medical Society in Vienna, showed his results which he had found independently.

He agreed with Goltz in his opinion that the labyrinth is a balancing organ for the head and indirectly for the whole body, but accepted endolymph flow as the mechanical stimulus.

His arguments were:

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1. Those from Goltz;

2. The tests of Flourens; he traced what really happens by cutting the canals, and assumed that the flow of the endolymph and the penetration of blood has a stimulating effect. In addition, reflexes would complicate the picture for the other canals;

3. Dizziness, when the ear is stimulated galvanically;

4. The tests of Purkyne;

5. The accurate regulation of balance in daily life demands an organ specially designed for it.

Thus far, he agrees more or less with Mach.

Concerning the endolymph flow, he later adopted the views of Mach.

He made an important addition to the theory by involving the otolith systems in the utricle and saccule in acceleration and the perceiving of position.

He later presented many good arguments [12-15] and advanced the following theories:

1. The otoliths, because of their higher specific weight, are as likely to stay behind because of acceleration as to exert a constant force under the influence of gravity or centrifugal force;¹

2. Lower animals have only otoliths and no semicircular canals; this is true only for moving animals. Animals lose their otoliths when they become immobile.

3. Like Mach, he sees in the similar character of the rotation and acceleration sensations and their similar proportions (the appearance of an after-sensation) a reason to believe that the same sort of sense organ is involved as in rotation. Since the experiment of Purkyne indicates that this must be located in the head, the labyrinth appeared most likely to be involved.

4. The maculae are sense organs, as is evident from their innervation, and are probably non-acoustic, since the clearly acoustic cochlea never contains otoliths.

Rotation, then, causes a combined stimulation of the semicircular canals and otoliths. Mach provided still more anatomical support for this theory, as we will see later on.

Shortly after Breuer, Crum Brown (Jan. 19, 1874) published his article on the sense of rotation and the anatomy and physiology of the semicircular canals of the inner ear [18]. He

¹ For the pike we determined the specific gravity of the saccule otoliths by suspending them in a mixture of chloroform and bromoform. We found the specific gravity to be 2.3.

So paid special attention to the sensations, accepting endolymph flow as a stimulus but also giving some new points of view.

Starting from the principle that one nerve can cause only one sensation, regardless of the kind of stimulus received, he attributed to each ampulla the ability to perceive only one turning moment. He explains this by pointing out that on both sides the canals are positioned as follows:

1. Both horizontal canals are more or less in the same plane;
2. The right posterior canal is in the same plane as the left anterior canal.
3. The left posterior canal is in the same plane as the right anterior canal.

Because of this, with the left and right labyrinths taken together, all six possibilities are taken into account (three dimensions, each with two directions), even if one accepts that each crista ampullaris can detect rotation in only one direction. He also found that the minimum perception threshold for different canals is not the same (later on, Van Rossum [59] made more accurate determinations).

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Even with all of this localizing of the sensation, there remained a weak point, since only galvanic stimulus of the labyrinth was known and this easily could be taken for a brain stimulus. Only a method of reasoning based on the anatomical construction and conformity of rotational reflexes and labyrinth stimulation in animals gave the final proof. If it were possible to examine people in whom one could expect defects in the organ and also to detect abnormality of their sensations, then this hypothesis would receive support. For this purpose, James [77] announced in 1882 the following observations made in deaf-mutes and claimed that of 519 deaf-mutes,

186 could not be made dizzy;

134 only slightly;

199 behaved rather normally. All but one of six normal subjects were included in the last category.

Floating in water, they were in danger of drowning due to lack of orientation; he saw some with their backs half out of the water and their heads bowed to their chests, looking frantically for the surface of the water. The help of others was needed to save them; therefore, they were completely confused about the position of the vertical since the latter is the direction in which the surface can be reached most quickly.

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Kreidl [43] conducted a more detailed investigation among 105 deaf-mutes. He discovered, in agreement with what Mygind [53] had found, on the basis of 118 post mortems on deaf-mutes described in the literature, that the percentage of non-func-

labyrinth agreed with that of serious anatomical deviations.

When rotated, 50% of the subjects had the eye nystagmus missing, which was almost never the case in normal subjects.

The statistics showed that 50% of the deaf-mutes had incomplete development of the semicircular canals.

The illusion of Purkyne was found to be missing in 13 of the 62 cases he investigated (21%).

None of these 13 had eye nystagmus. Here, too, there was an agreement with pathological anatomy, because abnormal vestibula are less frequent than abnormal canals. Later on [14], in connection with an investigation by Breuer and himself, in which it was apparent that rolling of the eyes determines the position of the vertical for our senses, he found that this was missing in the group mentioned.

We feel or see the vertical between the resultant of gravitational and centrifugal force and the real vertical (a resultant of 14° - 15° , for example, is seen as vertical at 8.5°); the rolling of the eyes measured by shifting of a linear after-image was also about 8° .

The abnormal manner of walking of many deaf-mutes has been known for a long time; they spread their legs, waddle, and drag their feet (the last is perhaps more because of deafness, since those who become deaf later on in life do the same). All those who showed pronounced symptoms in the previous categories also had disturbances in the gait, except for only one or two.

One can find an analogy in "waltzing mice". Here, too, there are congenital defects in the labyrinth: collapsed saccules and utricles, poorly developed nerve elements, etc. and similar disturbances in movement.

With this, however, we enter the field of reflexes and I would rather mention first the experiments related to the third group of sensations, i.e., those of standing. Yves Delage [20] began this study in 1886. At that time, all experiments were still aimed at answering the question of whether or not observation of rotation, acceleration, and the vertical was connected with the labyrinth. In order to answer this question, Delage followed this strange argument: if one can put the body in special circumstances and so create an illusion, one has the means to find the origin of this illusion; this also shows the origin of normal, non-illusory sensations. In my opinion, the possibility remains of a different cause for the regular sensations, which was altered in appearance by the additional factors in the test. However this may be, Delage for the first time has

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Investigated quantitatively the space sense, by which we are to understand the more or less correct image we form independently regarding the positions of the three dimensions. He positioned his subject opposite a target and had him (with his eyes closed) point to this target, or (by means of a stick) indicate the vertical, etc.

This proceeded with high accuracy when the subject was standing straight up. If he kept his head turned sharply to the right around a vertical axis (about 60°), then he pointed about 15° to the left of the target (A). On the other hand, if he imagined himself to have his body turned about 15° to the right (as compared to the real and correctly judged head turning of 60°), then in the latter case he pointed correctly to A, but placed a stick, held in the hand, in a slanted position on the breast at an angle of about 15° to the direction of the head rotation. This is true for the three rotational axes: vertical, transverse, and sagittal.

Both illusions are mutually exclusive. The first one is felt by the subject when he is new to the test; later on, he feels the second one. One can formulate this in general as follows: with strong head rotation, an illusion appears, presenting itself as a rotation of the environment at 15° to the rotation of the head, or as a rotation of the body at 15° to the head rotation.

One can formulate this in still another way, as done by Delage, namely: with a considerable turning of the head the subject has a correct idea of the angle which the related axis of the head forms with the axis of the body, but he turns his head 15° too far in relation to the surroundings and consequently gives the wrong indication, as mentioned by Delage.

Using experiments to explain this fact, Delage started by excluding the following points:

1. The cause is not that one senses the head movement too strongly and remembers this, because one can just as well hold the head still and turn the body only;

2. The error is not located in the muscular sensors, because the application of weights, which tighten the antagonistic muscles, does not change the illusion.

If we pay attention to the eye movement, we see that in rotation around the vertical and transverse axis the eyes turn 15° further to the side than the head does (at first, even more than 15° , but then they return and stabilize at 15°).

If only the eyes are turned strongly, this gives the impression that the head was turned 10° in the same direction; the

Error is then a little smaller because the neck muscles remain at rest. For rotation around the sagittal axis, this is not true, because now the eye compensates only partially, i.e., does not turn further than the head, but still the illusion is present. Delage claims this to be a proof of otolith function, because of a change in the action of gravity. Then one could imagine that, just as the other sensations of rotation were intensified by the position of the eyes, the same effect is now produced by a change in the action of the otoliths. He does not discuss this.

Delage first quotes a different visual illusion found by Aubert: a tilting (to more than 40°) of a bright vertical line against a dark background, caused by a marked leaning of the head. If the lights are turned on, the line becomes vertical. According to Aubert and Delage, the retina is the cause of this phenomenon. The eye gives an impression of position depending on where the image strikes the retina. Here, the vertical falls on the horizontal, but partial correction takes place:

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1. By rolling of the eyes in the direction of the head rotation;

2. By muscle sensations in the neck.

With the lights on, experience helps us to recognize the vertical line as such because it is parallel to other, different, known verticals (wall corner, closet and so on).

In the case of Delage, the eye movement is the cause; he proves this as follows:

1. Sitting in a vertically striped cylinder, he found that with maximal eye rotation in the horizontal plane, a line inclined at 15° was mistakenly believed to run in the direction of the movement.

2. Keeping the eyes straight in their orbits while moving the head can be achieved only after considerable difficulty; the illusion then disappears. The fact that this causes difficulties is explained as being due to the contradiction of this coordination with habit: when we turn the head, it is to see something at the side, and so on, and we look for this with the eyes. We then turn the head (most likely) as little as possible and make up for the difference with eye movements.

3. Turning the head and eyes in opposite directions causes the illusion to be maintained with eye rotation.

On account of this, Delage assigns the space sense to the:

1. Sense of touch;

2. Sense of sight;
3. Sensations in eye muscles.

The semicircular canals have nothing to do with all of this.

Much stronger illusions are produced by changing the position of the body. Delage laid a subject down on a board, which could be rotated by a hinge. /22

The differences between reality and illusion, produced by leaning the board backwards, are as follows:

Reality	Illusion
perpendicular	4° forward
5° backwards	perpendicular
45° backwards	slightly less than 45°
50° backwards	45° backwards
55-60° backwards	55-60° backwards
75° backwards	horizontal
90° backwards	10° past horizontal
30° past horizontal	vertical with head down

Here the eye movements compensate partly for the movement; this occurs because of the pressure felt on the skin, blood congestion, fear of sliding off, and so on.

Delage further repeated the experiments of Mach and concluded that not only a sense of acceleration but also one of speed (2° per second minimum) always indicate exactly where one is during rotation. He also states, "In rotational movements we are sensitive to variations in speed and not to variations in acceleration." Every speed change, however, requires a positive or negative acceleration.

He finds illusions regarding the position of the axis of rotation, by leaning the head during rotation, etc., but these are contrary to the static illusion (in a narrower sense), and are stronger.

He assumes that we would sense all rotation, even with stimulation of the semicircular canals, with the head upright. /23

With a shift in position, the illusion (because of turning of the head) does not change. Only very rarely does he sense an after-sensation. These two facts (according to Delage) prove that the acceleration sensation is something completely different from the rotational; when the labyrinth creates the first one as well, then the direction has to be pointed out, the same as with stimulation of the otoliths and head erect; accordingly, one would feel ascent, with the head bent forward at 90°, as

Regression. This is not the case. Therefore, he rejected the otolith theory of Breuer and found it more likely that acceleration was a general sensation having its origin in small shifts of place and pressure changes of the intestines with their partially liquid contents. He did not consider general orientation (as in homing pigeons) to be related to the labyrinth.

Except for the mechanical manner of stimulating the labyrinth, which was in itself completely developed (although many gaps remain to be filled, especially in the latter group), the galvanic method was applied once more by Hitzig and Exner. They saw reflexes show up again at the same time as with experimental animals, and sensations which were either the causes or the effects of them or were even created independently of them. An important recent contribution was the discovery of Barany (confirmed by Kubo) that rinsing of the middle ear with solutions at temperatures above and below body temperature brought about opposite sensations and reflexes.

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Apart from the strange effect, this treatment also has clinical usefulness, and the unquestionable merit of representing an ear-stimulus which does not completely exclude the possibility of including the brain in the reaction.

One can never prove this for the electrical stimulus.

§2. LABYRINTH REFLEXES

These reflexes, caused by passive and active movements or by experimental stimulation of the labyrinth, are:

1. Change of tonus in the muscles of the eyes, neck, trunk, and limbs;
2. Contractions of muscles;
3. Permanent tonus (also in rest position);
4. Vasomotor changes;
5. Vomiting and disability with violent stimulus.

One can summarize these in various ways.

For example, the first two mainly serve to preserve balance (according to Goltz and his followers) or weakening of the impressions (head nystagmus, observed by Ewald; walking against rotation as observed in ants by Bethe), or to fixing of the field of vision (head and eye nystagmus, corresponding head and eye positions).

The fourth and fifth involve cramps and paralysis.

/25

The history of this chapter starts with the observations of Purkyne [55]:

1. With rotation, the eyes stay behind in the plane of rotation and jump back (each time with much greater speed) approximately to their rest position (felt by putting a finger on the closed eyelids);

2. The illusion mentioned earlier, later on appeared to occur mainly with the intervention of a rolling reflex of the eyes.

Nagel [54] found these rolling movements by active and passive changing of the head position, in which he excluded joint movements. Here a partial compensation of the deflection is caused by the reflex. Flourens [29,30] in the meantime had described his fundamental experiments on animals, consisting of cutting the auditory nerve and semicircular canals, and stimulating the latter. He used pigeons and rabbits. His results were the following:

1. Such treatment of the canals leaves hearing unaffected.

2. Oscillations of the head occur in the plane of the affected canals.

3. Horizontal movements are controlled by cutting the horizontal canals, and similar movements of the body are affected by the other canals in their planes.

4. By cutting all canals or the auditory nerve, the animal no longer can stand up, and makes frantic movements.

He attributed to the organ a power "which contains and controls movement": disappearance of regulation caused disturbances. For this reason, he divided the eighth cranial nerve into acoustic and movement-regulating parts.

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As already mentioned, Menière found the same movements in his female patient, combined with dizziness. For the first time, he localized both causes in the labyrinth.

The experiments of Flourens were gradually extended over an entire series of animals. Every species requires its own technique; therefore, a description of the methods would take up too much space here. S. von Stein [67] gives a summary of this work up to 1894.

Birds remain the most suitable test animals, as their labyrinth is the most strongly developed, rather easy to reach and the reflexes are strong. A variety of stimuli were also used; chemical, thermal, electrical, and mechanical.

Soon it was observed that in all these experiments, the sensor was stimulated even when paralyzed. Extirpation could there-

fore be taken as stimulation of the nerve stump.

Reviewing the most important developments of the experiments, I must first mention Breuer [11], who succeeded in electrically stimulating each ampulla separately, and indicated that the galvanic currents in the experiments of Ritter, etc. affected the labyrinth and not the brain. The current had no effect in animals without labyrinths.

Ewald [24] thought the mechanical stimulus was even more pure and his experiments rank as sheer technical wonders; his long series of tests is completely convincing. He could generate currents in both directions in one specific canal in a pigeon which was under a screen and completely normal in its movements. The animal always showed reflexes associated with rotation in the plane of the canal. He found that by blocking the non-ampullar part of the canal, he could influence the other part with a pneumatic hammer which (by means of an air tube) could be set in motion at an arbitrary distance. If the endolymph flow was from canal to ampulla, he obtained a strong head movement, just as by rotation to the stimulated side; the head slowly returned to the center position; when the hammer moved backward, a weaker motion in the other direction followed.

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The question of which experiments have paralyzing effects and which ones are stimulating is thus solved definitely. By connecting a rubber tube to a canal and having a liquid inside press on the endolymph, Ewald could obtain positions completely contrary to those in pigeons without a labyrinth on that side or by pigeons with cut canals. Extirpation was therefore equivalent to paralysis and not stimulation of the nerve stump.

Similar effects were observed in both higher and lower animals. The lower animals often have the advantage of having their otocysts in direct communication with the outside world.

Prentiss placed iron filings in the auditory cavity of the lobster and added magnetism to the list of labyrinth stimuli. He also prevented Palaemon larvae, after they had molted, from collecting otoliths from the bottom, as they otherwise would do. These animals then showed disturbances in balance (swimming belly-up, etc.).

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Lee [48] and Bethe [6] choose fishes as test animals. Schrader [62] found a very easy method of removing the frog labyrinth through the mouth. Van Rossem [59] for the first time operated on turtles. Others used guinea pigs (Dreyfuss [22]), cats (Kreidl [44]), rabbits (C. Winkler), and dogs (Ewald).

In the manner of Prentiss, K. L. Schäffer [60] used tadpoles without operating. He discovered that the "rotational dizziness" under which Ewald summarized all phenomena generated by

Rotation appears at the same time with the development of the semicircular canals. In this manner, all kinds of peculiarities for diverse animals were added to the main rules of Flourens.

We should mention observations made by Ewald in pigeons and dogs a long time after the extirpation of the labyrinth. In the first place, it was evident that with retention and use of the eyes, the head of a patient with unilateral extirpation returns to a straight position. Further, he showed the following:

1. Muscle weakness on the affected side at the extremities, felt at the neck and spine (distribution is not very strictly arranged).

2. Absence of the reaction on the affected side with rotation and frequent weakening on the other; these latter symptoms differ in various animals, and may perhaps be a result of uneven phylogenetic development of the labyrinth.

After bilateral extirpation with retention of the cochlea, flying is no longer possible, eating and drinking are disturbed, the voice is weak, movements are alternately restricted and free; the animals show weakness of the muscles, no further reaction on the turntable, but unimpaired hearing. Because of this, Ewald suggested a labyrinth tonus, in which almost all voluntary muscles participate; this tonus would also be maintained by the labyrinth during rest.

/29

In man, we have already seen the same type of disturbances in the experiments of James and Kreidl with deaf-mutes. There were defects in their sensations as well as in their reflexes.

Von Stein [68] completed the investigations by using persons who had contracted diseases of the ear during their lives (rather than deaf-mutes) to study their static positions. He paid special attention to locomotion and found that many ear patients showed the following deviations (always with eyes closed):

1. Rocking when standing with feet together, especially forward and backward. The same was observed when the subjects stood on tip-toe.

2. Coordination disturbances in the legs, crossed and uncrossed.

3. A smaller tumbling angle on his goniometer. This instrument of von Stein's is nothing more than a piece of wood on which the patient stands and which is slowly tilted by raising one of the ends. For every plane, a normal person has an angle of inclination at which (with eyes closed) his sense of balance fails and he tumbles over. It showed that ear patients could withstand less tilting than the average. This gives a simple method for expressing quantitatively (in number of degrees) the function of the labyrinth.

/30

4. Rapid tiring occurs when hopping, playing leap-frog, etc.; they jump in a zigzag manner with alternately large and small jumps (labyrinth jumps), which according to von Stein are completely typical.

5. They cannot stand on one leg and turn around.

This is not ataxia, because it disappears when the eyes are opened.

The scope of this series of phenomena is expanded by observing the changes in the footprints of labyrinth patients and measuring the force necessary to cause such a person to topple over (Wanner).

Von Stein measures this by the weight and length of a pendulum striking the shoulder of the patient. The force required is least on the affected side. Later on, he announced still another case [69], in which he attributed acceleration of the breathing rate and pronounced visual dizziness in an ear patient to the labyrinth.

Egger discovered two patients in the Salpêtrière. According to the theory of Mach-Breuer, one had normally functioning semicircular canals, but suffered from a defect of the otoliths; the other case involved the opposite situation.

Many additional details are desirable where man is concerned, especially experiments with people in which one can definitely assume a defect of one labyrinth, but they are almost completely lacking, because such certainty is so difficult to obtain; this experiment could determine if one labyrinth serves only one set of three directions in man, and if not, the extent to which the sensations and reflexes in each canal show preference for one direction.

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From some of his observations, von Stein concluded that the labyrinths could not substitute for each other. In animals with otoliths and semicircular canals, it was not possible to remove by operating, or to stimulate, only the first system because the canals run into the utricle and the latter is always involved. Sewall [63] thought he could more or less avoid these difficulties by using sticklebacks and sharks. He observed reflexes produced by stimulating the ampullas. However, after opening up the saccules, he found that the sticklebacks had an inclination to turn on their longitudinal axis in the direction of the lesion and to sink to the bottom. The latter may perhaps be regarded as a purely otolithic phenomenon.

§3. SUMMARY OF THE THEORIES

Recalling how well we have succeeded in coordinating the observed facts, we must agree that Mach was completely right in his belief that all studies of motion sensations had to be based on the fundamental laws stated by him. The main qualities of the sensations of rotation and acceleration are obtained directly from this.

With respect to the basis of these sensations, there is less possible doubt; however, there are still big gaps in the details. /32

One can accept as a fact that passive rotation and stimulation, in the manner of Ewald, have exactly the same effect.

In man, these reflexes have been combined with sensation, so that we can accept the Mach theory as completely proven, especially if one adds the observations for the ear patients of Kreidl and von Stein.

The otolith theory cannot boast of facts that prove it immediately, because (as we noticed) tests with animals with the same indisputable clarity are not possible.

Here, more proof must be provided by discussion. Breuer [12,15] has tried to find support for his theory in anatomy, coupled at the same time with observations of the semicircular canals. He assumed that these are formed so that only small divergent currents, coming from the canals, strike the crista ampullaris. The crista is perpendicular to the canal axis, but outside it. The stronger the current, the smaller will be the fraction that acts as a stimulus. Because of this, the organ is protected against too strong a stimulus. Here he still speaks about currents, but assumes them (as Mach does) to be infinitesimally small; the macula utriculi is protected by a septum against pressure changes transmitted from the canals. Hensen [40], who still believes in the acoustic theory, because of the inequality of the canals, points out that every irregularity in the labyrinth of the pigeon (which he chose as the most developed and most easily accessible) is cancelled by another irregularity. The mathematical structure of the organ is discussed in great detail: according to Breuer, the functional parts of the canals are all of the same length. (Crum Brown and Van Rossem, however, found differences in sensitivity). The hairs on the cristae are (according to Breuer) glued together by a cupula terminalis; the ideas of Hensen et al., who took the latter to be artificial, were disproved by him on the basis of his preparations. With this, the possibility of an acoustic function is immediately disposed of. Also, we can better realize now that moving this cupula must stretch the hairs and cells, even if the motion is minimal. A slow return from the stretched position must then

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explain the prolonged sensation after the stimulus comes to an end.

Even more important are the anatomical arguments for his otolith theory, which have already been mentioned to a certain degree. Some of them, drawn from comparative anatomy, are:

1. The otolith organ is the original one, from which the semicircular canals as well as the cochlea have developed.
2. There is a direct neural connection between the otoliths and the lateral organs in fishes; the same has been pointed out in *Ctenophora* by Engelman.
3. Animals without a cochlea cannot hear.
4. Otolith tests with animals result in the same reflexes (special rolling of the eyes) as in man, which cannot lead to a reaction of the semicircular canals (i.e., tilting the head).
5. In animals with three otolith structures, the latter are located in three planes, just as the semicircular canals are. Breuer also found one sliding direction for each otolith, especially in fishes [12]. This sliding occurs along the longitudinal slot of the otolith, in which the whole papilla nervosa is covered by a membrane. /34

In man, the three-dimensional principle is maintained in spite of the loss of one of the systems due to its development into the cochlea. If the clivus Blumenbachii is located horizontally, there are two possible directions for vertical and horizontal movement: from lateral back to medial front (utricle-otolith) and vertically (saccul-otoliths). Acceleration in all directions can be sensed by a combination of the two organs. In animals with a lagena, the otolith located in the latter is vertical and the otolith in the saccul is horizontal; if the lagena has been transformed into a cochlea, the otolith in the saccul is elevated.

The plane of the clivus is also more or less the same as that of the horizontal canal. This establishes still another connection between the two parts of each labyrinth.

Breuer [14] studied the illusion of Purkyne once again, and found that inclination of the head by $\pm 15^\circ$ relative to the axis (parallel to the mass acceleration) caused the illusion to disappear. He also pointed out the difference in compensation by rolling of the eyes.

In the case of rotation, this compensation amounts to $\pm 0.6^\circ$ of the angle formed by the resultant of the gravitational and centrifugal forces with the vertical; with inclination of the head, this amounts to only 0.1° of the angle traversed (Nagel, [54]);

in the case of other muscles, as in skating, this was immediately and completely compensated. From this we may conclude that the passive position when standing upright, combined with the effort to maintain balance, does not strengthen the reflex. The illusion is most striking in the frontal plane, which may have some connection with flying (this has no significance for man, of course).

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These matters must remain unexplained for the time being.

According to Breuer and Nagel, forward motion should produce a feeling of being bent backward, because the otolith also presses in the occipital direction. Bending backward, however, is coupled with rotation. This can suffice for distinguishing both. The relationship between position and acceleration will soon be discussed. Skin and intestinal sensations have the same effect, as we see from the experiments of Delage with the inclined board. These experiments should be repeated under water in order to collect data excluding the skin sense, and to evaluate the possibility of an organ in the head which can perceive position. There is considerable evidence in favor of this. We think first of all of the experiment of Purkyne; either the labyrinth immediately reveals the position of the vertical, or the eye reflex occurs, which must have a very particular origin in the head. An experiment by Kreidl with deaf-mutes showed that reflexes and sensing the vertical always go together.

The experiments of Delage also favor the possibility of a sensation based on the position of the eyes. We notice, however, that Delage's explanation regarding observation of eye movement becomes invalid when the head is rotated around the sagittal axis. This indicates another source of observation of position. The otolith may be involved, and perhaps the movement of the head around the transverse axis as well.

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Barany [3, 4] felt that a sensing of the eye nystagmus was involved in a sensation of rotation. As far as we were able to ascertain, by putting fingers on the closed eyelids, the nystagmus had already finished before the sensation. There is also the case of after-sensation produced by fixation of the open eyes; this does not last as long. This question could be settled by using photography; the apparatus would have to rotate with the subject. Along this same line of reasoning, we should note that observation of the vertical is required in order to make practical use of this, even if the position of the limbs with respect to one another is known from muscle sensations. The data given by James offer striking proof of this. We see that otoliths are especially necessary to animals which live in water, because for them the pressure of the water compensates for gravity. In addition, however, the semi-circular canals cannot function without the aid of the otoliths, as we can prove by an analysis of the rotation stimulus and its sensations.

The accelerated rotational motion consists of two parts (with

the labyrinth assumed to be eccentric):

(a) An accelerated tangential progression.
(b) Accelerated centripetal progression. If the rotation has been smooth, we then have:

(a') A uniform tangential progression;
(b') An accelerated centripetal progression.

The entire set of sensations consists of four parts:

1. In a narrower sense, the rotational sensation is produced in the semicircular canals, because a and b differ in absolute size, depending on their distance from the axis;
2. Detection of a by the otoliths; /37
3. Detection of b and b' by the otoliths;
4. Detection of the position of the head. When the rotation is smooth, 1 and 2 disappear but 4 remains, changed by the detection of b' .

The thresholds of the first three components have different positions: 1 is lowest, followed by 2 and then 3.

This has not been determined for 3, as far as we know; however, it is known that the thresholds in the frontal plane have the lowest position. The illusion of Purkyne appears in this plane, when the same rotation fails to produce it in the other planes.

If the conditions in 3 were not as represented, one would initially have a feeling of centripetal motion at the beginning in addition to the rotation, when b began to produce an effect. Since this would be incompatible, it would probably produce a mixed sensation.

We now feel ourselves to be rotating, and this excludes the other, weaker feeling. We do not sense 3 until the sensation of rotation has disappeared.

The four parts are completely involved only in the case of rapid rotation. Since different head positions cause different canals to be stimulated each time, with the rotation being otherwise even, only the sensations in 4 above will reveal the plane of rotation. The semicircular canals in themselves can only perceive the location of the axis of rotation with respect to the labyrinth. If rotation is carried out first with the head bent backwards 65° to the sagittal axis, and then with the head bent forward 25° to the vertical axis, there will be no possibility of making a distinction because in both cases the horizontal canals are in the plane of rotation and are therefore stimulated in exactly the same way. In the case of both rotations, the other four canals remain completely at rest. /38

The same holds true, mutatis mutandis, for the observation of the direction of progression.

Only the observations mentioned under 4 above can provide a solution regarding the motion of the entire body. Delage assumed that his experiments prove that a couple of rotations of this kind were not recognized. He went so far as to say that each rotation stimulation was sensed completely according to its position with respect to the head alone. If the position of the head were changed each time on a regular turntable with a vertical axis, the rotation should be observed in different planes. This is not at all the case; the rotation is always sensed accurately, with only a few mistakes. However, the distance from the axis is not known. Changing of the position during rotation causes confusion, as Mach has already mentioned; this confusion originates in the fact that canals are now affected which were previously at rest; the others do not show an after-sensation, and confusion results. However, if a rotation is repeated over and over in the horizontal plane, with different positions used from the start, these positions are accurately recognized just as in the case of progression.

It should be worthwhile to repeat his experiments, using the anatomic structure of the labyrinth as a guideline, which Delage did not.

The best arrangement would be to rotate:

(1) Around the transverse axis, with the head inclined horizontally to the right (45°);

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(2) Around the sagittal axis, with the head inclined horizontally to the left (also at 45°); gravity has the same effect in both cases and the same canals (rear right and upper left) are stimulated.

If we rotate the body with both labyrinths in a position as central as possible, then the progressive motions in the centripetal acceleration will be very small, and we will sense an equivalent sensation of rotation.

If this were not the case, then we might think that the observation of the direction of progression would also lend its sensation of space to the rotation. According to Delage, this is also felt in all positions of the head without error. If this is eliminated by sitting in a central position, only a combined feeling of the position of the head and rotation can provide a solution. Here too, the very strong relationship between the four sensations in general indicates a common origin in the same sense organ.

It is still strange that a force can be felt on one occasion as acceleration and as a feeling of stationary position on another. We probably sense a sudden impact as acceleration, while constant

pressure is sensed as something stationary. This means that the explanation which Mach proposed, i.e., that we would have the feeling of sinking deeper and deeper on a planet smaller than the Earth, is eliminated; we would only have such a feeling if the gravity were not to decrease gradually but rather rapidly.

We must therefore assume the existence of a sense organ which produces uninterrupted sensations. /40

Ewald explains this as well as his permanent labyrinth tonus, by a vibrating movement of the head, caused by fluctuations of the tensions of the neck muscles, which supposedly creates periodic changes in the pressure of the otoliths [23].

In my opinion, the following observations contradict this theory: when the muscle sense fails us (e.g., when we awake after a long rest, and are unsure regarding our environment, we still know the position of the head precisely. Eye movement and eye blinking, however, may help with this. As we have seen, Delage ascribes everything to an observation of the position of the eyes. In any case, the trembling of the head is then abolished, without any information being provided by the skin regarding the location of the pressure; no change is unnoticed in the accuracy of observation.

If a sensation in addition to the reflexes indicating the position of the head is to be felt, it must have a character more or less resembling the muscle sense. The sensations are so weak, however, that its absence may be noted only when disturbances result; again, experiments may be especially designed to reveal it. A patient may rarely be found who complains that he cannot walk well because he does not know the exact position of his legs. Because the head is almost always sufficiently well oriented by the eyes, only a possible failure of the usual reflexes or unusual behavior (as in the deaf-mutes of James) will reveal anything out of the ordinary. In this case, there was a breakdown between the sensation and the response, which (according to Ziehen [73, 74]) also exists on a different level which can be referred to as sensitivity to sensation. This must be the case with all continuous sensations, or they will have a disturbing effect. Coupled with the rotation, one now has the curious phenomenon that the sensation of rapid rotation is combined with a distinct impression regarding the plane of rotation; the sensation of the position of the head is distinct in itself, but involves much less sensitivity. /41

These peculiarities of the organ make the dissenting theory of Von Cyon [19] more understandable. He rejects the theory of Mach-Breuer, and states that the cerebrum and cerebellum produce the proper sensations of motion (acting as organs, just as Purkyne believed), calling the labyrinth the space organ.

He formulates this as follows:

1. The actual orientation in the three planes of space, i.e., the selection of the directions in which our motions should take place, as well as the coordination of the nerve centers required for detection and maintenance of the directions, constitutes the exclusive function of the semicircular canals.

2. The regulation of the degrees of innervation which this requires, both for these centers as well as for those which control the maintenance of equilibrium and other voluntary movements, takes place primarily through the medium of the labyrinth.

3. The sensations produced by the stimulation of the canals are sensations of direction. They lead to conscious sensations only when the attention is directed to them. The sensations give us direct information regarding the three principal directions in space, the sagittal (forward and backward), vertical (up and down) and lateral or transverse (right and left).

Because his experiments with animals often yielded negative results, he used this fact as a basis for rejecting the theory of Mach-Breuer. Breuer [13] took the trouble to repeat the experiments in order to discover the mistakes made by Cyon. The following examples will be sufficient: /42

(1). Cyon claims that a frog, when rotated passively, certainly does not always turn its head. Breuer shows that the reflex can easily be suppressed if the animal is fastened down firmly or held. This has nothing to do with the labyrinth.

(2). Cyon says that flow in the canals does not always lead to head movement. Breuer points out that his methods (absorption of the perilymph by blotting paper, etc.) are entirely insufficient for producing a definite flow in the endolymph.

For his part, Cyon ascribes the head positions after extirpation and so on, to changes in the impressions regarding space which are felt by the animal. He felt that the semicircular canals and otoliths are stimulated by motion, noise, and impressions of vision; from all of these stimuli, the sensation of space can be separated, with each canal sensing one dimension, and in this way our impression of space is formed.

Breuer countered this argument by pointing out that persons lacking a labyrinth are suitably oriented in space by the rest of their sense organs. The quality of space is a direct property of every sensory stimulus (the sensation of touch, e.g.), and there is no need for a separate organ to sense this. /43

Recently, Cyon dealt with his theory in detail once again, now connecting the sense of time with the labyrinth. We are unable to discuss this work here because of its late arrival and considerable length.

Breuer is willing to give Cyon credit for drawing our attention to the significance of the labyrinth for our image of space.

According to Breuer, however, this is only a part of the sensation of movement; to this we would like to add that the observation of the position of the head with respect to the vertical is almost purely a space image as Cyon sees it. In this respect, Cyon joins the others in drawing sharp distinctions regarding the significance of motions in space for our sensations. To the extent that there is a separate perception of space, this is not the case for the other sense organs.

Ewald, too, has his own point of view distinguished by the importance which he attributes to the muscle tonus under the influence of the labyrinth. Here once again we have an analogy between the static sense and the muscle sense. The existence of this tonus is clearly evident from the conditions of his test animals, deprived of labyrinths observed a long time after the operation. Changes of this tonus must therefore produce the reflexes in rotation, and so on.

In general, the positions after an operation and reflexes with passive movement can be interpreted as follows:

(1) Contraction

(a) Because of disappearance of a "restriction" (Flourens with paralysis or extirpation of the labyrinth.

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(b) Starting with a labyrinth which has not been operated on or has been stimulated by rotation, etc.

(2) Loss of tonus

(a) Because of paralysis or extirpation (encountered mainly at neck and trunk; not encountered in limbs);

(b) Because of stimulation.

This loss of tonus is then unevenly distributed among the muscles (the extremities are weak and stretched; flexors therefore have less tonus than extensors). Ach [1] felt that he could distinguish a separate otolith tonus (the one encountered in the trunk).

The usefulness of the reflexes would be:

Maintenance of balance (Goltz, etc.);

Decrease in sensation;

Fixing of the field of vision.

Therefore, when head nystagmus is prevented in the pigeon, the after-effects are more violent; when the eyes are open, the nystagmus is weakened when the environment rotates and is strengthened when the environment does not rotate. The field of vision is fixed as far as possible. Finally, according to Ewald, the labyrinth has a considerable influence on the coordination of eye and

head movements: a dog deprived of its labyrinth, trained prior to the operation, performs poorly afterwards in attempts to catch pieces of meat thrown at it. Confusion due to lack of sensations of movement may perhaps explain this.

According to him, the eye nystagmus is a labyrinth reflex only to a partial extent; the reaction is the result of the different position which is thus obtained. /45

The permanent tonus places us in the same difficulty as the permanent observation of the head position; since we cannot assume as in the muscle sense, a centripetal stimulus that supports the tonus (experiment of Brond-Geest), Ewald looked for this stimulus in the labyrinth itself.

Ewald detected a "lashing movement" of the hairs on the cristae; he calls them "tonus hairs"; we can eliminate this concept if we join Breuer in recognizing a cupula terminalis, which connects the hairs.

In the chapter dealing with the sensations, we found that the sensation of the position of the head is still a problematic one.

In addition, we cannot presently give any explanation of the manner in which a motion is analyzed by the labyrinth and reproduced in our consciousness.

I have tried to indicate the difficulties which are encountered in discussing rotation.

The hypothesis regarding the origin and purpose of labyrinth reflexes also leaves a great amount unexplained.

CHAPTER II

OTOLITHS

When a guinea pig is moved in a vertical line with sufficient acceleration (± 2 m per sec), its head remains behind in the usual manner and returns to a straight position when the motion becomes uniform or ceases. /46

The reflex time for this otolith reflex was determined as follows: the animal was placed in a small box lined with cotton, and its head was put through an upright oval opening in the side. The box was then placed on a scale which was suspended from a rope. This rope passed over a pulley anchored 3 m above the floor and the scale was raised by pulling on the other end of the rope. In this way, the scale, box, guinea pig, and some instruments for recording were balanced against weights attached to the other end of the rope.

These weights were suspended in a frame with a pulley on the bottom. In order to ensure that the scale and guinea pig would soon reach terminal velocity and would maintain it, a fly-wheel driven by an electric motor was used as the mode of power. While the wheel was still coming to full speed, a small wooden disk attached to the wheel wound up a rope.

This rope passed over the pulley under the weights and could be tightened with a steel bar. The bar was first pulled up, and when the fly-wheel reached its full speed, it struck the abovementioned pulley, so that the weights were suddenly pulled downward and the scale and guinea pig were pulled upward. /47

In order to stop in time, a brake was pressed against the fly-wheel. The brake consisted of a moveable pole attached to the floor, covered with felt and mounted in the plane of the wheel. This pole conducted the current to power the fly-wheel; the current was disconnected during braking.

The recording was accomplished as follows:

A piece of tape was fastened to the head of the guinea pig between the eyes, after shaving the area. A wire connected to this

tape transferred the head movements to a pointer, with a reduction of 3 to 1. The pointer wrote on a small kymograph placed on the scale. The scale was held on both sides by wires to keep it from swinging; the wires were kept under tension by heavy weights, which were in turn kept from swinging by a layer of moss which just touched them where they hung close to the floor. The wires were also used to conduct current from a timer mounted on the floor to the scale, and from there to a spring contact rubbing against the wires.

This current passed through a signal marker mounted on the scale.

Finally, the motion of the scale was recorded by the interruption of another current, indicated on the kymograph by a second pointer.

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The large pulley supporting the scale and its counter weights, as well as the two conducting wires, was connected to a portion of the frame of the rotating apparatus, which was supported by a rod between the floor and the suspension shaft to prevent vibration and bending.

All the experiments proceeded as follows:

The pointers and contacts were adjusted, the timer and fly-wheel motor were started, as was the kymograph. The disk was suddenly pulled up, and after it had moved ± 2 m, the fly-wheel was stopped by interrupting the current of the motor.

Because the guinea pig was constantly moving, it was necessary to wait a favorable moment for starting the experiment. However, the reflex motion is of sufficient magnitude (despite the reduction of the pointer-lever system), that it is unmistakable on the paper.

The speed of the scale was measured with a stop watch.

The measured reflex times were as follows:

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TABLE I. ACCELERATED PROGRESSIVE MOTION

Guinea Pig A		
Speed (reached in ± 0.3 " per second)	Reflex time in seconds	Average
1.40 M.	0.1; 0.11; 0.12;	0.11
1.50 "	0.1; 0.12; 0.13;	0.12
1.75 "	0.1; 0.1; 0.18;	0.13
2.— "	0.09; 0.08; 0.05;	0.07
2.20 "	0.1; 0.14; 0.1;	0.12
2.50 "	0.09; (0.25); 0.13;	0.11
General Average 0.11		

Guinea Pig B

Speed (reached in 0.4")	Reflex time	Average
1.50 M.	0.1; 0.14; 0.12;	0.12
1.60 "	0.11; 0.1; 0.09;	0.1
1.85 "	0.08; 0.09; 0.12;	0.1
2.10 "	0.09; 0.1; 0.1;	0.1
2.40 "	0.1; 0.07; 0.16;	0.11
2.40 "	0.11; 0.13; 0.08;	0.11
General Average 0.1		

Hence, the measured reflex time is ± 0.10 sec in both animals².

The reflex times for motion of the animal from top to bottom are given in Table II. /50

The small changes which must be made in the set-up need not be described.

TABLE II. ACCELERATED PROGRESSIVE MOTION

Guinea Pig A

Speed (reached in 0.3")	Reflex time	Average
1.40 M.	0.12; 0.11;	0.11
slightly more	0.08; 0.1; 0.13;	0.1
" "	0.1; 0.11; 0.09; 0.2;	0.12
" "	0.1; 0.08; 0.1;	0.09
" "	0.19; 0.12; 0.11; 0.2;	0.16
2.50 M.	0.2; 0.16; 0.12;	0.16
General Average 0.12		

² Regardless of the considerable acceleration, a motion without latention, amounting to a mechanical falling behind of the head, was out of the question.

Guinea Pig B

Speed (reached in 0.4")	Refelx time	Average
1.50 M.	0.13; 0.1; 0.07;	0.1
slightly more	0.18; 0.12; 0.1; 0.18;	0.14
" "	0.1; 0.14; 0.09;	0.11
" "	0.2; 0.11; 0.2;	0.17
" "	0.25; 0.12; 0.16;	0.17
2.50 M.	0.13; 0.2; 0.05;	0.12
General Average 0.13		

Therefore, we obtain a reflex time of ± 0.12 sec for both animals.

The test apparatus described above had the following disadvantage; the rope with which the scale was pulled up, slid because of the sudden pull and made the motion of the scale irregular. I also abandoned my attempts to make the stimulus momentary, since its useful effect is small. Therefore, I sought a different motive force whose energy and duration could be controlled completely.

/51

I felt that the problem could thus be solved pneumatically. Therefore, I took a tank containing 300 liters which could withstand a pressure of six atmospheres. This tank was to serve as a supply of energy after being filled. A hole 2 cm in diameter was drilled in the cover. A perpendicular tube 2.5 m long was threaded into that hole and fastened to the wall at the top. A second tube was placed within this first tube; the bore of the second tube was sealed at the bottom and extended slightly above the top of the tank. The abovementioned scale was connected to the top of the inner tube.

The flow to this compressed-gas elevator was regulated by two taps located just above the cover of the tank. The top tap was first adjusted to a certain final velocity of the platform; when the tank was filled to a certain pressure from a bottle of liquid carbon dioxide and the top tap was adjusted, the platform could be given the desired motion by suddenly opening the lower tap. It was possible to achieve accelerations from 1.3 to 140 cm/sec lasting from 0.04 to 2 sec by using different pressures in the tank and loading the platform with different weights (from 1 to 20 kg).

/52

Friction was reduced by greasing the inner tube, and recordings indicated that the motion for all velocities which were not too low started with uniform acceleration. The recording were made on a kymograph, rotating on a vertical shaft beside the table. This was easy, since the tank could be placed in the first floor and

the length of the tube was such that the table just reached the level of the second floor corridor. A stationary pointer and a time marker (0.1 sec) were both connected to the table and wrote on the kymograph. This made it possible to read the type and duration of the acceleration immediately.

In the first place, it appeared to be uniform. The large, constant force of the compressed carbon dioxide was not influenced by the friction. The flow of carbon dioxide was restricted by the position of the tap and the acceleration suddenly became zero after a certain period of time. Despite the large and uniform force, the duration of the acceleration (excluding friction) was limited. At first the acceleration was nearly uniform, but this changed in an immeasurably short time into a uniform velocity because of the rising of the platform.

The platform was kept from rotating while going upward by having a slot on the side of it engage a vertically suspended wire. I began by repeating the earlier experiments as well as those for determination of the reflex time of the guinea pig's head movements.

The moment of departure of the platform was recorded by opening a contact; this made a mark on the small kymograph placed on the scale with the guinea pig. The movements of the animal, including the time, were recorded on this kymograph.

/53

These determinations produced the following results:

TABLE III. UNIFORM ACCELERATED PROGRESSIVE MOTION

Guinea Pig 1

Acceleration (cm per sec)	Reflex time	Average
4.3	0.08; 0.1; 0.12; 0.05; 0.09; 0.14;	0.09
5.2	0.13; 0.14; 0.09; 0.1; 0.1; 0.1;	0.11
8.3	0.1; 0.2; 0.18; 0.1; 0.1; 0.08; 0.06;	0.12
9.4	0.1; 0.1; 0.1; 0.1; 0.1; 0.1; 0.08;	0.1
11	0.12; 0.14; 0.16;	0.14
16	0.14; 0.16; 0.18;	0.16
83	0.2; 0.1; 0.16;	0.15
132	0.1; 0.1; 0.06; 0.09;	0.09
General Average 0.12		

Guinea Pig 2

Acceleration (cm per sec)	Reflex time	Average
4.6	0.1; 0.05; 0.07;	0.07
6.3	0.2; 0.18; 0.12;	0.17
9	0.09; 0.11; 0.1;	0.10
13	0.13; 0.1; 0.1;	0.11
16	0.13; 0.17; 0.09;	0.13
137	0.1; 0.1; 0.12;	0.1
General Average 0.13		

Guinea Pig 3

/54

Acceleration (cm per sec)	Reflex time	Average
4.6	0.11; 0.16; 0.14;	0.14
4.9	0.4?; 0.1; 0.09;	0.1
7.2	0.08; 0.1; 0.18;	0.1
9	0.05; 0.1; 0.12;	0.09
13	0.07; 0.2; 0.16;	0.14
19	0.08; 0.1; 0.18;	0.12
68	0.13; 0.09; 0.07;	0.09
125	0.1; 0.1; 0.1;	0.1
General Average 0.11		

Average of the three tests: 0.12 seconds.

The apparatus also lends itself very well to a determination of the absolute sensitivity of the otolith organ, because of the possibility of setting the stimulus precisely.

I employed the various combinations of strength and duration of stimulus which were just able to evoke a reflex.

When I thought that I had found such a combination by eye, the motion of the head was recorded as a check, and at the same time the motion of the scale was recorded on the second kymograph.

These determinations had the following results:

TABLE IV

/55

Guinea Pig 1		Guinea Pig 2		Guinea Pig 3	
accel.	dur.	accel.	dur.	accel.	dur.
5	0.40	8.1	0.35	5.4	0.40
6.3	0.35	7.2	0.30	5.3	0.40
7.2	0.35	6.9	0.30	8.1	0.40
7	0.30	7.3	0.25	7.3	0.03
7	0.25	7.3	0.20	10.2	0.25
9.4	0.2	10	0.20	8.7	0.20
9.6	0.20	9.2	0.20	9.2	0.18
10	0.20	11	0.20	9.6	0.15
27	0.15	11.3	0.18	12.2	0.10
29	0.15	28	0.15	15.1	0.1
30	0.15	25.3	0.12	45	0.1
50	0.1	30	0.1	70	0.1
28	0.1	45	0.1	120	0.08
60	0.1	90	0.1	130	0.08
125	0.08	85	0.09	110	0.08
132	0.05	130	0.07	115	0.08
240	0.04	139	0.07	135	0.06
237	0.04	140	0.05	140	0.06
		142	0.05	137	0.06
		140	0.05	142	0.05
		137	0.05	260	0.04
				200	0.04

Since it is not possible to find any connection between the reflex time and the amount of acceleration in Table III, we can assume this time to be 0.12 sec in each case.

The force used during this interval alone is sufficient to evoke a reflex. If, as in the sense of pressure, we assume the stimulus to be proportional to the product of the time and the force, we then find the minimum value for the unit of mass as follows: /56

Guinea Pig 1	Guinea Pig 2	Guinea Pig 3
$0.12 \times 5 = 0.60$	$0.12 \times 6.9 = 0.83$	$0.12 \times 5.4 = 0.65$

These represent the products of the reflex time and the smallest acceleration found which would still cause a reflex.

The acceleration still in force after the reflex time is con-

sidered superfluous and therefore is not included.

The absolute amount therefore depends on the component parts of the otolith organ, especially on the specific gravity of the otoliths relative to that of the endolymph surrounding them.

We can see from the table that as soon as the duration of the stimulus falls within the reflex time, the intensity of the stimulus must increase enormously if a reflex is to follow. The most economical arrangement is therefore an even distribution of the stimulus over the total reflex time. The force which still acts afterwards is not required for the minimum reflex and only extends the reflex. The greater accelerations last for a somewhat shorter period of time than the smaller ones; this was due to a peculiarity of the apparatus and can be explained by the manner in which the carbon dioxide was admitted to the tank.

The tube attached to the platform had to be filled and moved rapidly upwards, so that the supply of carbon dioxide increased to fill the space. However, this favored the reaching of very short acceleration times.

In the following curve (Fig. 1), the relationship between the

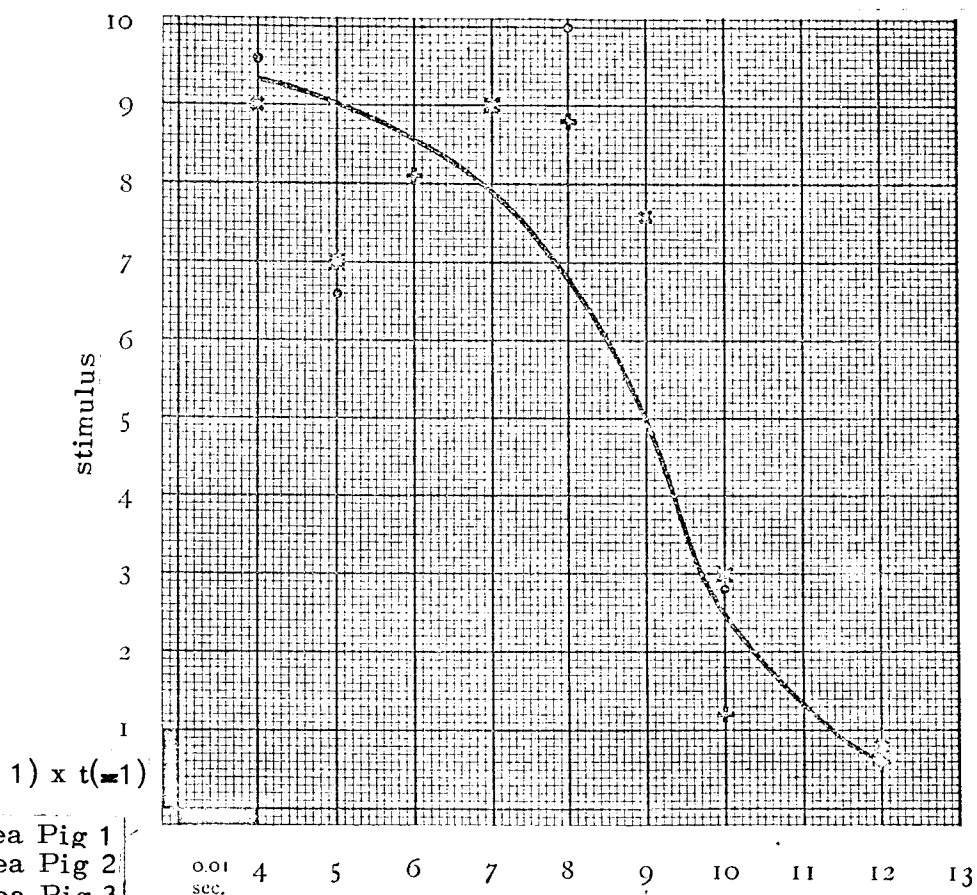


Fig. 1. Duration of the Acceleration

magnitude and duration of the stimulus required for a minimum reflex is shown.

The time is shown on the abscissa, while the ordinate shows the relative intensity of the stimulus.

The curve is plotted on the basis of the data given in Table IV, using only the portion falling within the reflex time. The smallest accelerations are used, multiplied times the reflex time. /58

The uncertainty in measuring small values such as 0.04 sec can be blamed for the fact that the curve does not show a more constant slope within the reflex time.

The minimum stimulus values have been selected.

The actual minimum may be somewhat higher, but this is not important for the mutual relationship determined here.

CHAPTER III

SEMICIRCULAR CANALS

§ 1. REFLEXES IN ANIMALS

a. Reflex Time of Eye Nystagmus in the Pike.

The skin and skull of a pike were removed above the labyrinth /59 until the contours of the horizontal canal were visible. On both sides, fine needles were inserted into the cartilage of the labyrinth cavity, 0.75 cm apart. An induction current was fed through one of the needles; it passed through the labyrinth, stimulating it, and then passed out through the other needle.

A signal marker in the primary circuit indicated the moment of contact.

A piece of thread was passed through the conjunctiva of the eye of the animal; this thread was tied to a lever pointer fitted with a counter weight, to which it transmitted its motion. The signal marker and this pointer, along with a time marker (0.1 sec) wrote on a kymograph.

The induction apparatus was the same as that used by J. Gewin, with water interruption (Thesis, Utrecht 1906). The current was recorded momentarily. The eye moved quickly forward and slightly upward. This eye reflex could be related specifically to the /60 working of the horizontal canal. As we have said before, the otoliths and canal functions cannot be distinguished accurately.

The deflection of the pointer attached to the eye showed two periods: one of them was not noticeably latent and was very small; the other increased with reflex time.

Apparently the first was caused by current loops directly stimulating the eye muscle nerves or the eye muscle itself. No attention was paid to this.

Reflexes marked with (*) showed this motion. A potential of two volts was used.

TABLE V

/61

Pike 1

position of the coil	reflex time(in sec)
55	0.15; 0.2; 0.19; 0.2; 0.2; 0.08; average 0.17
45	0.04; 0.04; 0.05; 0.05; average 0.05
10	0; 0; 0;

The last measured motion is probably caused by the current alone, and perhaps the one before the last as well; what was measured, then, was the latency. A period of 0.05 sec is somewhat long, but because of the operation, the animal was already in an abnormal condition by that time.

In the next experiment, the search for the horizontal canal proceeded more rapidly.

Pike 2

position of the coil	reflex time(in sec)
55	0.18*; 0.16*; 0.18*; 0.20*; 0.17*;
45	0.16*; 0.14*; 0.14*; 0.18*; 0.14*;
25	0; 0.01; 0.04; 0.01; 0; 0;
10	0; 0; 0.1; 0.13; 0.1; 0; 0;

If we use only those curves in which the proper reflex is clearly distinguished from direct stimulation of muscle, the average value is 0.17 sec.

Pike 3

position of the coil	reflex time(in sec)
30	0.1*; 0.1*; 0.1*;
55	0.1*; 0.1*;
40	0.18*; 0.1*; 0.18*;
20	0.1*; 0.1*; 0.1*;
10	0.1*; 0.1*; 0.1*;
0	0.1*; 0.1*; 0.18*; 0.1*; 0.1*; 0.1*; 0.18*; average 0.12 sec

There is no connection between the strength of the current and the reflex time, other than the influence of the current. The average of the three experiments is 0.15 sec.

Summation of the induction stimulus is very slight. I used as a primary current, the current from the timer coils, so that I received a stimulation at periods of $1/20$ of a sec (10 times opened and 10 times closed in one second). This was recorded by the eye pointer as an electrical signal several seconds long; stimulation at a rhythm of 50 times per second (25 closings and 25 interruptions) produced tetanus. /62

b. Frogs

If a frog is seated at rest and rotated around a vertical axis, the labyrinth produces a reflex motion of the head which is a rotation opposite to the first rotation, regardless of whether it is sitting with its head turned away from or toward the center. If the disk is turning to the right (clockwise), the animal always turns its head to the left; if it is sitting with its head pointed away from the center, the head reflex is in the opposite direction to the rotation of the disk. If the animal is seated facing the center, then the reflex is in the same direction as the rotation. The same is true at positions in between. For an animal in which eyesight plays a more important role, a high rim must be placed around the disk; otherwise, the reflex is weakened or strengthened depending on the position of the animal (facing the axis or turned away from it).

The direction of the head axis is of course immaterial for the horizontal canal; the reflex must be the same at all times, with the exception of the view. Only the centrifugal force should be able to produce sensations through the otoliths. We attempted to study the nature of this motion in greater detail and to record it.

1. Reflex Time

/63

We first determined the reflex time as follows:

The frog was placed on a small disk, with the hind legs fastened to a small board by soft cords.

Tightening of the cords was avoided in this and all the following experiments because it retards the reflex.

A needle was inserted into the cartilage of the upper jaw and carried a wire for transmitting electricity. This wire conducted the current through the axis of the disk.

The head of the needle was placed against a small metal sheet; the latter was also connected to an insulated copper wire and trans-

mitted the current through the raised tin border of the disk and onto the outside by rubbing against copper brushes, through a signal, and back to the element. If the animal now moved its head to the side, the current was connected and a signal was recorded.

The kymograph connected to this system started up at the same time as the disk.

We saw to it that the drum and the disk started at the same time. The disk reached its terminal velocity almost immediately.

In this way, we obtained the following data (all times are given in seconds).

TABLE VI

/64

a. At the start.

rotation speed (per second)	reflex time	average
18°	0.7; 0.7; 0.7; 0.7; 0.8; 0.8; 0.8; 0.8; 0.8; 0.8; 0.9; 0.9; 0.9;	0.8
36°	0.6; 0.6; 0.6; 0.6; 0.6; 0.6; 0.6; 0.6; 0.6; 0.6; 0.9;	0.6
72°	0.5; 0.5; 0.5; 0.5; 0.6; 0.6; 0.6; 0.6; 0.6; 0.6; 0.6;	0.6
80°	0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.5; 0.6; 0.6;	0.5

b. Halting

rotation speed (per second)	reflex time	average deld.
18°	0.6; 0.7; 0.7; 0.8; 0.8; 0.8; 0.8; 0.8; 0.9; 0.9;	0.8
36°	0.6; 0.6; 0.6; 0.7; 0.7; 0.8; 0.8;	0.7
72°	0.6; 0.6; 0.6; 0.6; 0.7; 0.7;	0.6
80°	0.4; 0.4; 0.4; 0.5; 0.5; 0.5; 0.5; 0.6; 0.6;	0.5

It therefore appears that a higher speed of rotation produces a shorter reflex time.

It will be clear from the experiments described below that this can be ascribed to an increased rate of motion with more rapid turning of the disk, and not to a shortening of the reflex time with more rapid rotation. The distance between the two contacts (the needle and the metal plate) is made in a shorter time, so that

the reflexes are recorded earlier, even with equal reflex time. This is still noticeable even if the contacts are brought as close as possible to one another.

/65

This error could be avoided only by recording the entire motion.

A rotating disk, like the one described in the thesis of Van Rossem (p. 81 et seq) was used for this purpose.

The frog was fitted with an indicator (a needle in the upper jaw, to which was attached a straw with a paper point). The distance from the head to the point of the indicator was 8 cm. This indicator recorded the complete motion on a horizontally rotating drum placed in front of the frog and also resting on the disk. The animal was fastened in the manner described above. Most of the time, the front legs could be left free. The influence on the reflex, produced by tying the animal down was scarcely noticeable.

The moment at which the disk began to turn had to be recorded accurately. This was done by interrupting an electrical current. Two inflexible contacts, one on the disk and one beside it, were allowed to rest against one another; they separated when the disk rotated.

The interruption of the contact was marked by a signal magnet on the drum rotating with the disk.

The following data applies to three frogs.

TABLE VII

/66

speed of disk	reflex time (in 1.10 sec) average	Number of observations
8°	3.3	8
10°	3.3	4
15°	2.9	7
18°	2.2	9
22°	2.2	4
24°	3.2	6
30°	2.2	8
35°	3.2	8
72°	3.1	3

We failed to find any relationship between the final rotation rate and the reflex time. Hence, we can consider a reflex time of 0.3 sec as being average for all speeds.

In order to determine whether the reflex time was influenced by the cerebrum, we made a number of tests with frogs in which the connection between the mid-brain and the medulla oblongata was severed with a scalpel.

Prior to the operation, the reflex time was 0.3".

TABLE VIII

I. One hour after operation			
rotation	reflex time(0.1")	average	
10°	4; 4; 4; 4; 5; 5; 5; 5; 5; 5; 5; 5; 6; 6; 6;	5	
28°	2.5; 2.5; 2.5; 2.5; 2.5; 2.5; 3; 3; 3; 3; 3; 3; 3.5; 3.5; 4;	3	
45°	2.5; 2.5; 2.5; 3; 3; 3.5; 4; 4; 4; 4; 4; 4; 4.5; 4.5; 4.5; 4.5;	4	
II. Next day			
3°	3; 3; 3.5; 3.5; 3.5; 4; 4; 4; 4; 4; 5; 5; 5; 5;	4	
15°	2.5; 2.5; 3; 3; 3; 3; 4;	3	
20°	2.5; 2.5; 2.5; 2.5; 3; 3.5;	2.5	
30°	2; 2; 2.5; 2.5; 3; 3; 3; 3; 3.5; 4;	3	
40°	2; 2; 2.5; 2.5; 2.5; 2.5; 2.5; 3; 3; 4;	2.5	

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Once again, we see no connection between the numbers in the first and third columns; therefore we can use the following averages: for I: 0.4 sec; for II: 0.3 sec.

The animal showed a longer latent period immediately after the operation, but returned to normal on the following day. This can probably be ascribed to the inhibitory effect of the recent injury.

2. ANALYSIS OF HEAD MOTION

We studied the reflex motion at different rotation speeds,

especially the magnitude of the deviation.

TABLE IX

/68

rotation final speed	deviation	average deviation
14°	1.5; 1.5; 1.5; 1.5; 1.5; 1.5; 2; 2; 2; 2; 2; 2; 2;	1.75
18°	1.5; 1.5; 1.5; 2; 2; 2; 2; 2; 2.5; 2.5; 2.5; 2.5; 2.5;	2.1
26°	1.5; 1.5; 1.5; 1.5; 2; 2; 2; 2.5; 2.5;	1.9
36°	1.5; 1.5; 1.5; 1.5; 2; 2; 2; 2; 2; 2; 2; 2; 2; 2;	1.9
51°	2; 2; 2; 2.5; 2.5; 2.5; 2.5; 2.5; 2.5; 3; 3; 3; 3; 3;	2.6
72°	2; 2; 2; 2.5; 2.5; 2.5; 2.5; 2.5; 2.5; 3; 3; 3;	2.5
90°	3; 3; 3; 3; 3; 3; 3; 3; 3; 3.5; 3.5; 3.5; 3.5; 3.5; 3.5; 4; 4; 4; 4;	3.4

averages:

rotation speed 14°—18°—26°—36°—51°—72°—90°.

deviation(in cm) 1.75—2.1—1.9—1.9—2.6—2.5—3.4.

If the data are plotted on graph paper, with the final speeds on the abscissa and deviation on the ordinate, we see that the latter increases more or less linearly with increased speed.

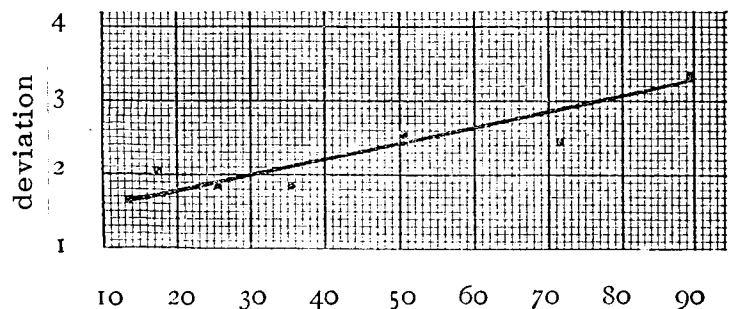


Fig. 2. Final Rotation Speed.

A comparison of the liveliness of the motion provides a completely different picture. Each curve was divided into five equal parts by a method which will not be described here; a line was drawn between the extreme points. The angle formed by this line with the abscissa was measured.

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TABLE X

speed	degrees of angle				average
14°	26	31	31	22	27.5°
18°	33	37	30	18	29.5°
26°	36	31	23	18	27°
36°	40	34	24	19	29.25°
51°	36	40	34	26	34°
90°	37	39	44	28	27°

These numbers were averaged from ± 10 observations for each speed. The extremes were never more than 4° apart.

Four frogs were used.

/70

We see from the table that the nature of the motion remains nearly the same at highly different speeds; this is still more evident if we use graph paper to plot curves made up of four equal parts, whose slope corresponds to the average angles determined previously.

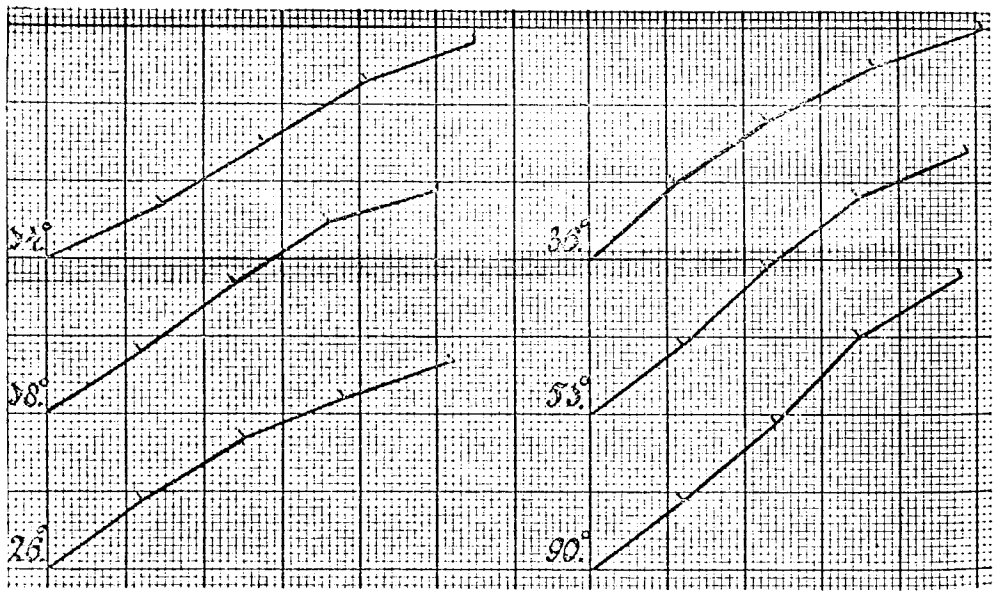


Fig. 3

The curves for the speeds of 14° , 18° , 51° and 90° show the best agreement, in that the motion achieves its maximum value after the start but decreases again toward the end. At speeds of 26° and 36° , the beginning is the steepest after which the curve slowly becomes horizontal.

Mainly, however, all six curves are the same, so that we can say that a faster speed of rotation causes the frog to turn its head further; however, this greater deflection is achieved by a motion of the same type. Therefore, the animal requires a proportionately longer time to move its head through a longer distance. /71

The latter result led us to make a more detailed investigation of the nature of the stimulus. Therefore, we attached an indicator to the turntable and recorded the beginning of rotation on a kymograph, located horizontally next to the apparatus.

The curves obtained in this manner clearly showed that lower final speeds were reached in relatively short times; at the faster speeds which we were using, however, because only then was the reflex of the frog sufficiently strong, the accelerations were smaller and showed little variation.

Instead of being able to use this series of experiments to investigate the effects of stimuli of different strengths, only the influence of the duration of the stimulus was detected.

final speed (per sec)	duration of acceleration (in sec)
14°	1
18°	1.5
26°	3
36°	3
51°	3.5
90°	4

In addition, the acceleration was not uniform.

Only the uniform acceleration produces a constant stimulus on the labyrinth. It was necessary to regulate the magnitude and duration of this uniform acceleration. Uniform acceleration can be obtained by using a constant force. /72

Gravity was not suitable because the transmission mechanisms required with such a system introduce considerable friction.

This friction increases with speed, and hampers the uniformity of the acceleration; it causes the stimulus to decrease instead of proceeding smoothly. We therefore needed an apparatus with minimum friction, powered by a force which was constant, easily regulated, and readily disconnected. For this reason, we returned to the use of the small turntable mentioned above. It was mounted on a bicycle axle and therefore turned easily; because of its high (20 cm) tin rim, it was highly suitable for completely excluding the influence of vision; in the case of the frog, however, this influence was already small. The disk was set to rotating by a

stretched coiled spring, one end of which was fastened to the center of the disk and the other end of which was mounted firmly in a tripod.

The spring was twisted by the motion of the disk, and the resultant tension produced driving force when the disk was released.

Smoked paper was fastened to the outside of the tin rim, on which a time marker recorded 0.1" intervals, so that the motion could be recorded.

The distance (s) covered with uniform acceleration (a) is $s = 1/2 a t^2$; the distances are therefore proportional to the squares of the times. By measuring the distances and comparing them with those produced by uniformly accelerated motion, we could determine those positions of the spring which would produce the various uniform accelerations. Obviously, in order to regulate the duration of these various stimuli, a design had to be found in which the tension of the spring could be eliminated at predetermined moments and the disk could continue rotating with uniform, non-accelerated motion. The stimulus would then cease.

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In order to eliminate the torsion suddenly, the upper end of the spring was connected to a shaft, which was free to rotate between two plates mounted 2 cm apart with very little friction. Attached to the shaft and resting on the top plate was a small cross piece, which was arrested by a lever when the spring tightened, thus causing the entire mechanism to remain stationary by stopping the disk regardless of the tension. The disk was then released; 0.5 seconds later, the lever was also released by closing an electrical circuit, so that the spring was suddenly released at the upper end and the disk continued to rotate without acceleration. We performed the two motions (releasing the disk and switching on the current with a key) by listening to a metronome ticking at half second intervals.

The motion of the turntable disk appeared to be uniformly accelerated, but the release of the spring caused a disturbing vibration in the apparatus. This gave me the idea of using the spring construction of the "pantokymograph" of Engelman (see Fig. 4).

In the latter, a coil spring is mounted in a housing whose horizontal border is perforated by a number of holes. Pins can be placed in these holes. One pin pushes the catch (located perpendicular to it,) forward and away from the shaft; the other serves to limit the action of the spring, because it is caught a short time after the kymograph is released. The first pin was shortened after the first rotation of the disk, since the catch could pass over the end of the pin as it rotated and then turn beneath it freely during subsequent rotation. For this purpose, the small spring in that pin was removed. The duration of the acceleration could be regulated with the other pin; this was accomplished by pushing

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a rubber tube onto it, whose thickness advanced the moment of catching. The rod of the kymograph was unscrewed and mounted on an oak board, just as before, and placed beneath the turntable. A shaft was connected to the center of the turntable disk and was moved by the coil spring on the top like the shaft of the kymograph.

The regular spring had to be replaced by a weaker one, since the speed was otherwise too high. Moreover, the reduction in the force of the spring with relaxation had to be reduced to a minimum by winding the spring very tightly; its force then remained constant while the disk was being driven³. An interval of 0.5 seconds was selected for the duration of the acceleration.

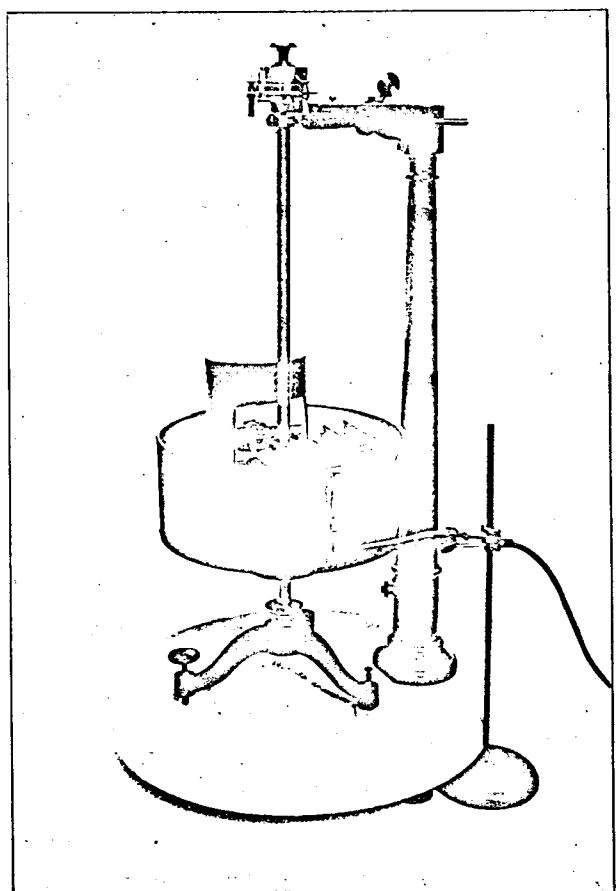


Fig. 4.

During this period, the spring acted and was then caught, after which the rotating disk (turntable) continued to rotate at a uniform speed. /74a
/75

Just as in the earlier case, the motion of the rotating disk was recorded by pasting smoked paper on the outside and having an indicator mark 0.1" intervals on it. As expected, perfect uniformity was not obtained because the friction was initially high, then decreased, and later increased once again as the speed increased; it therefore worked against the acceleration.

The results of the measurements can therefore be summed up as follows: in the beginning, the disk moved slowly and then accelerated uniformly (as perfectly as could be desired), and then slowly lost its acceleration; before the decrease of the acceleration had made significant progress, the spring had already been arrested, so that the effect of friction did not

³ We were fortunate to have the assistance of Mr. D. B. Kagenaar, Sr., the manufacturer of the original devices, in making these changes. A description of this will be found in the thesis of Dr. W. A. Boekelman (Utrecht, 1894).

cause a curve of the plotted distances to vary considerably from the theoretical curve.

Different accelerations could be obtained by varying the mass of the disk and adjusting the tension of the spring. Disregarding friction, the acceleration is $a=k/m$; both k and m were variable. Therefore, some of the heavier parts of the disk were removed and replaced by aluminum; any increase in the mass therefore had a greater effect. This increase was accomplished by placing weights on the disk, inside the raised edge as far as possible from the center.

When the curves were measured, this apparatus appeared to run almost ideally. An acceleration of 8 cm of the outside rim (31°) per second, which was suppose to give theoretical distances in the following proportions: /76

1 4 9 16 25

in other words, with values of:

4 16 36 64 100

it actually gave:

5 17 38 64.5 98.

Therefore, it was a little too fast at the beginning, and a little too slow after that.

We could obtain accelerations of 20° - 70° per second for 0.5 seconds.

In these experiments, the animal was tied as before to a small board, but now facing the center; we have already seen that this could not have an effect on the labyrinth. The influence of the vision was also excluded by the tin rim around the disk, and also by a cardboard tube with a lid which was placed over the animal. The tube had an opening in the front to let the indicator through. This opening is somewhat enlarged in Figure 4 in order to make the frog more visible.

The indicator rotated on a vertical shaft, next to the shaft of the disk, and was 4.5 cm long on the side of the animal and 4 cm long on the other side. The motion was therefore reduced slightly. A thin needle was inserted in the nose cartilage of the frog, and a small pair of tweezers was connected crosswise to it; this was connected in turn to an indicator which wrote on a small drum. On the other side of the axis of the needle, it was tightened by a very flexible rubber band against the head motion. The frog now pulled on the end of the needle which was placed to the right of its head.

The rotation was clockwise; because the animal was placed facing the center, the reflex also was in this direction. We first ensured that the disk made the same motion with equal spring positions and loads; this proceeded flawlessly. /77

Since the instrumentation was so perfect, a more distinct target for the experiments could be set. An obvious one was to determine the ratio of the reflex to the stimulus, similar to the law of Weber-Fechner for sensation. The considerable deflection of the reflex and the possibility of recording it completely, including the accurate measurement of the stimulus, made this a highly suitable case in which to study the relationship⁴.

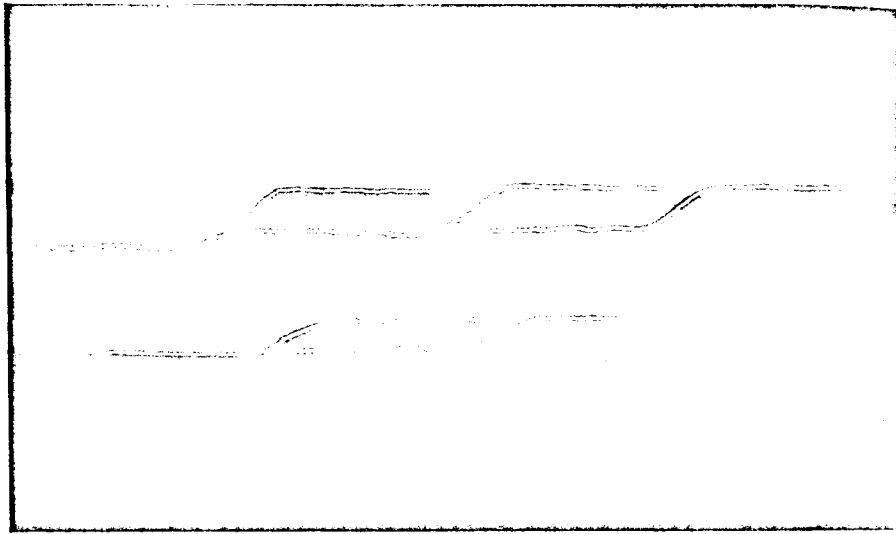


Fig. 5.

⁴ In the literature, I found the dissertations of Stirling (Ludwig's Arbeiten, 1874, p. 245); like Pfluger, he emphasizes the expansion of the reflex by increasing the stimulus.

Wayenburg (thesis, Amsterdam, 1897) attempted to find the law of Weber in the reflexes produced by chemical stimulation of frog skin, just as was done by Langelaan (Archive fur Physiologie, Supplementary Volume, 1903, p. 370); he pointed out some deviations, however. Pari (Archives italiennes de biologie, Vol. 42, p. 109) found, in addition to extension, intensification of the reaction for all the muscles involved, while Sherrington (Journal of Experimental Physiology, Vol. 1, p. 67; Journal of Physiology, Vol. 31, p. 334 and Vol. 34, p. 1) did find steady relationships but not such as could be expressed in a single formula. He restricted himself to reporting his curves, as did Hermann (Archiv fur Anatomie und Physiologie, Vol. 61) and Merzbacher (Pflugers Archiv, Vol. 81, p. 604).

We used the method of minimum perceptable differences, judging the difference in reflex by deflection and steepness of the curve.

Figure 5 shows some examples of these curves.

/78

Even a superficial observation will show a striking difference between the shape of this curve and the one found earlier. It now rises ratherly abruptly from the abscissa and maintains the slope acquired in this period until the maximum deflection is reached; no summation of the stimulus, as expressed in increasing steepness of the slope, was observed. We will see later on that in man there is a pronounced summation in the senses. The entire reflex is determined by the slope and deflection. In addition to the slope, the deflection also depends on the duration of the stimulus. Since a small error was involved in the regulation of the duration, I thought it better to consider only the slope, since the latter is the direct expression of the effect of acceleration as a function of its magnitude. This slope had a small convexity, caused by the rotation of the indicator. This could be ignored.

/79

The kinks noted earlier in the curves were therefore a reflection of increasing or decreasing acceleration. With uniform acceleration, the reflex is uniform in rate and the slope can therefore be expressed by a single number. For example:

Acceleration = 34.8° per sec.						Average
Deflection:	1	1	1.5	0.95	2	1.2 cm
Slope:	26°	26°	25°	27°	26°	26°
Acceleration = 30.9° per sec.						
Deflection:	0.95	0.95	0.9	1	1.5	1 cm
Slope:	25°	25°	26°	25°	23°	25°

We considered the difference in reflexes of this magnitude to be barely noticeable. However, if the accelerations are compared, we obtain a ratio of 9 to 8. The threshold of differentiation is therefore 1/9 or 11%.

We recorded the reflexes in three frogs with the following values of acceleration:

34.8° and 30.9° (ratio of 9 to 8)
and 69.6° and 61.8° (same ratio).

In the following table, we have listed the figures referring to the motion of the disk; for comparison, we have added the theoretical values beneath the accelerations found at the edge (see p. 47):

/80

acceleration (a) = 18 = 69.6° per sec.

	9	37.5	84	155	227
theor.:	9	36	81	144	225

$a = 16 = 61.8^\circ$ per sec :

	8	32	72	128	200
theor.:	9	34	72	132	198

$a = 9 = 34.8^\circ$ per sec.:

	4	17	39	71	111
theor.:	4.5	18	40.5	72	112.5

$a = 8 = 30.9^\circ$ per sec.:

	3	16	37	66	102
theor.:	4	16	36	64	100

If we take into account the unavoidable measurement errors and the errors produced in the recording of the time by the friction of the time marker against the smoked paper, as well as the uncertainty regarding the period of the indicator movement in which the disk began to move and the resultant increase in the error produced by these small variations, we can consider the speed of the disk (on the basis of these figures) to be influenced by pure uniform acceleration.

The experiments were conducted as follows: first of all, acceleration 18 was recorded; the disk was then loaded until a value of almost 16 was reached. More and more weights were added until 16 was reached, after which still more weights were added.

/81

The same was also done for 9 and 8. We now investigated the slope values to determine whether any noticeable differences could be found for 16 and 8; these differences were not chosen too small because of the measurement error).

In the table listing the results, the acceleration was given in a specific number of centimeters. The numbers 18, 16, 9 and 8 therefore indicate only the ratio of the acceleration; the angle values refer to the slopes of the curves.

TABLE XI

acceleration	Frog a. angles	averages
18	36°; 39°; 36.5°;	37°
> 16	37.5°; 20°; 40°;	32°
16	30°; 40°; 45°;	38°
< 16	30°; 25°; 30°;	28°
9	29°; 25°; 32°;	28°
> 8	28.5°; 30°; 31°;	30°
8	29°; 26°; 27°;	27°
< 8	25°; 26°; 20°;	23°
Frog b.		
18	34°; 40°; 28°;	34°
> 16	30°; 20°; 35°;	28°
16	38°; 28.5°; 36°;	34°
< 16	34°; 25°; 27°;	28°
9	25°; 28.5°; 21.5°;	25°
< 8	26°; 23.5°; 29°;	26°
8	35°; 20°; 23.5°;	26°
< 8	15°; 20°; 22°;	19°
Frog c.		
18	39°; 41°; 42°;	40°
> 16	30°; 38°; 39°;	36°
16	28.5°; 35°; 38°;	33.8°
< 16	27°; 25°; 24.5°;	25°
9	20.5°; 22°; 24°;	22°
> 8	23°; 25°; 21°;	23°
8	22°; 24°; 18°;	21°
< 8	16°; 17°; 22°;	18°

/ 82

The numbers differ considerably, and the same is true of their averages. It therefore remained questionable whether a constant proportion of angle values and acceleration could actually be concluded from this.

We changed the method of experimentation. For some frogs, the rate of the reflex was measured with an increasing series of

accelerations. Time intervals of 0.1 sec were recorded on the drum when the load was decreased and the acceleration increased.

These results are given in the following table.

TABLE XII

/83

acceleration	Frog d. angles	averages
4	14°; 13°; 20°;	16°
5	28°; 20°; 23°; 22°; 19°; 20°; 35°; 30°; 25°;	} 24.7°
6	22°; 17°; 18°; 25°; 24°;	
7	27°; 34°; 29°; 32°; 31°;	31°
8	40°; 35°; 37°; 40°; 38°; 35°;	} 37.5°
9	34°; 35°; 35°;	
	Frog e.	
5	10°; 13°; 15°;	12.6°
7	25°; 25°; 30°;	26.6°
8	23°; 20°; 25°; 32°; 38°; 33°; 30°; 28°; 33°;	} 29°
11	35°; 38°; 33°; 32°;	
15	40°; 42°; 35°;	42°
	Frog f.	
4	15°; 16°; 20°;	17°
5	20°; 22°; 19°;	23.6°
7	21°; 23°; 19°;	21°
8	20°; 20°; 20°; 18°;	20°
9	30°; 38°; 30°;	32°
13	30°; 40°; 40°;	36°
15	45°; 40°; 45°;	43°

averages of the three frogs:

/84

acceleration	angles
4	15.6°
5	20.3°
6	21.2°
7	26.2°
8	28.8°
9	33.3°
11	34.5°
13	36°
15	42.5°

The following table (XIII) presents an opportunity for comparing the two series of figures.

The tangent of the angles is the deflection divided by the time, because the abscissa is drawn by the kymograph.

The tangent therefore indicates the rate of the reflex.

TABLE XIII

I.	II.	III.	IV.	V.	VI.
accel.	accel. × 4.	angles	log. of the accel. : 0.0365.	accel. × 7.	tan. of the angles (× 100).
4	16	16.5	16.5	28	29
5	20	20.3	19.1	35	36
6	24	21.2	21.6	42	38
7	28	26.2	23.1	49	48
8	32	28.8	24.7	56	54
9	36	33.3	26.1	63	65
11	44	34.5	28.5	77	68
13	52	36	30.5	91	72
15	60	42.5	32.2	105	91.5

The first four columns provide an opportunity for comparing the angle values with those of the acceleration and its logarithm. /85

No clear relationship can be seen between the figures in Column III on the one hand and those of Columns II and IV on the other.

If, in addition, we also double the numbers in the fourth column (Log. acceleration: 0.0365) and compare them with the tangents, we noted that they do not increase in the same way. Columns V and VI show the greatest degree of agreement, at least until acceleration 10 (= 38.7° per sec) is reached; at this point, we approach the maximum, which differs considerably from one animal to the next. In the case of frog d, e.g., the increase above acceleration 9 failed to produce any further changes in the reflex.

The principal conclusion that can be drawn from these experiments is that the rate of the reflex (measured by the tangents of the angle formed with the abscissa by the line drawn by the frog) is directly proportional to the degree of uniform acceleration.

A logarithmic relationship such as we were inclined to accept on the basis of the first series of experiments could not be found in this second, more accurate series. In the first experiments, accelerations 18 and 16 were too large to permit comparison of re-

reflexes. Because the animal became restless, the reflexes showed too much variation. It is better not to exceed $\pm 40^\circ$ per second, taking into account the initial friction which does not permit a much greater acceleration during the first 0.1 second, so that the stimulus is not completely smooth during this period.

Figure 6 shows graphically the relationship between the acceleration and the reflex rate. The relationship is expressed by a nearly straight line for intermediate reflex values. /86

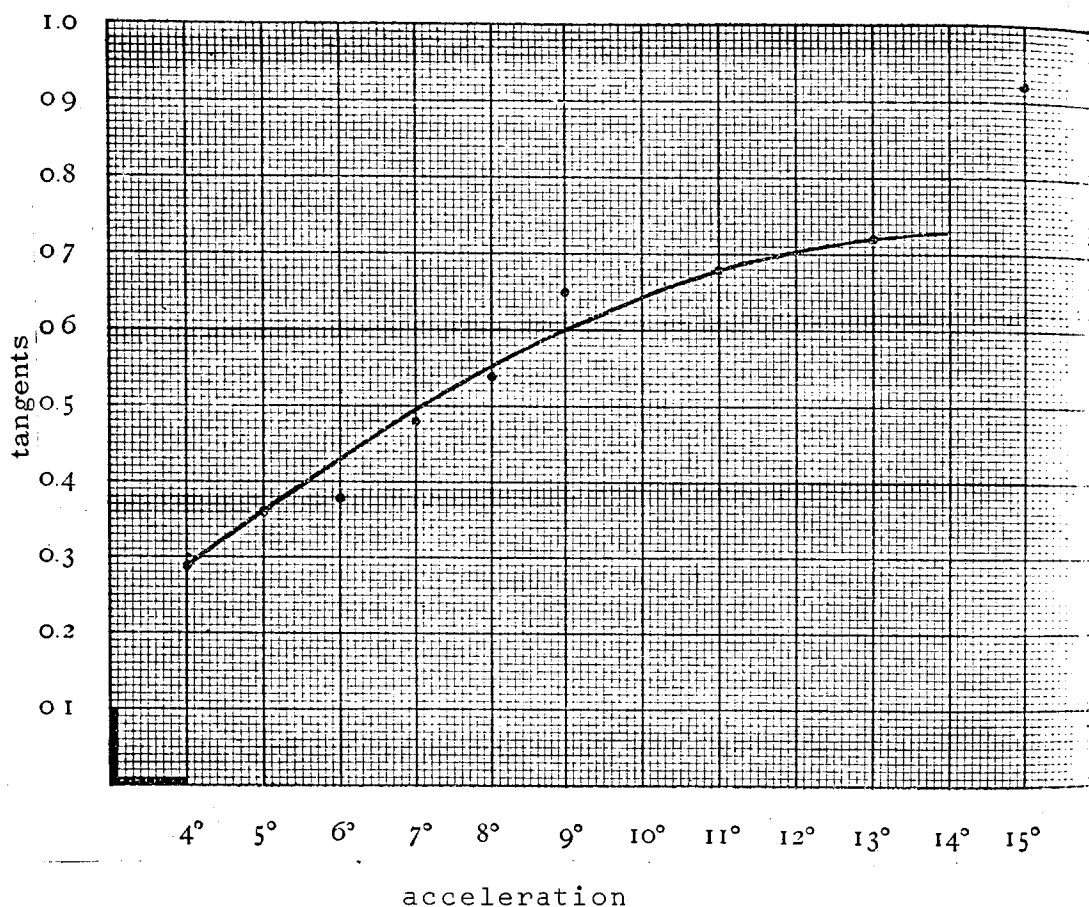


Fig. 6.

In the case of the maximum acceleration, the reflexes are intensified by a fright reflex, resulting from the noise produced by releasing the turntable. This reflex is also found if the disk is halted suddenly and rotation stops. During rotation, the influence of noise is sometimes shown by a small extra peak at the start. /87

The curves produced by the animals in the manner described above have a different character if the acceleration is continued.

Acceleration was produced by decreasing the resistance in the

electric motor circuit. It could be measured as follows: the large disk was provided with a spring contact which touched two others (located on the floor) during each rotation.

This was recorded on the rotating drum mounted on the disk, along with the duration and the head motion.

This method did not allow us to find any relationship between acceleration and curve shape that could be expressed numerically.

The frog moved its head from the middle line, as in the case of a brief acceleration, continued to oscillate around the furthest point, and then returned to the equilibrium position when the disk stopped. In addition, the head was often lifted; motion was not completely horizontal.

The animal was also often restless.

It therefore appeared that constant accelerated motion is a stronger stimulus for evoking the reflex, but many arbitrary (or in any case, different) influences prevent the effect of the stimulus from being read accurately from the curve.

We used the following accelerations:

/88

Acceleration per second	Duration in seconds
16	4
9	8
8	9
4	12
5	15

We did not succeed in reaching the point at which acceleration failed to produce any further effects owing to fatigue of the organ. Since the acceleration had to be rather high, the speed of the apparatus became too rapid after a period of time and had to be reduced.

This meant that the acceleration could also not be made uniform.

The only thing that can be concluded from this experiment is that the organ did not become oblivious to the stimulus within 15 seconds.

c. Reflex Time in the Turtle.

The large turntable (disk) was used for the measurements.

In these experiments, we had to move the disk manually in order to start the experiment at the exact moment when the turtle held

1. head motionless. The recording needle was placed in the skin of the animal's nose.

The rotation acceleration was measured at $\pm 40^\circ$; time is given in tenths of seconds.

Turtle 1:

2:2; 3:3; 4; 5;

average 3.

Turtle 2:

1.5; 2; 2; 2; 2; 2; 2; 3; 3.5; 4;

average 2.5.

Reflex time is therefore 0.27 seconds.

d. Reflex Time in the Guinea Pig.

/89

In this case also, the large turntable was rotated manually.

The guinea pig was placed in the small wooden box, with its head protruding through a horizontal oval opening on one of the short sides. A small cap was placed over the animal's head to cover its face and keep the needle in place. This was necessary in the guinea pig, since the vision has a significant inhibitory effect on the reflex.

Rotation equals $\pm 40^\circ$; time is given in tenths of seconds.

Guinea Pig 1:

1; 1; 1; 2; 2; 2; 3; 3; 3.5; 3.5; 3.5;

average 0.23".

Guinea Pig 2:

1:1:1:1.5:1.5; 2:2:2; 3.5:3.5:3.5;

average 0.2".

Different Direction

1:1; 1.5; 2:2:2:2:2; 3:3:3;

average 2".

Overall average equals 0.2 seconds.

§2. REFLEX TIME OF NYSTAGMUS MOTION IN MAN

After we had oriented ourselves by means of certain experiments and assured ourselves of the fact that complete darkness was required for study of nystagmus during its execution, we used magnesium-flash photography to determine the reflex time in man first.

The camera was mounted in front of the turntable (see Fig. 7).

/90

The line drawn on the turntable passes across the shaft and across the points of rotation of both eyes.

To show their position relative to the turning point, the eyes

have been drawn on a somewhat larger scale than the rest of the picture for the sake of clarity.

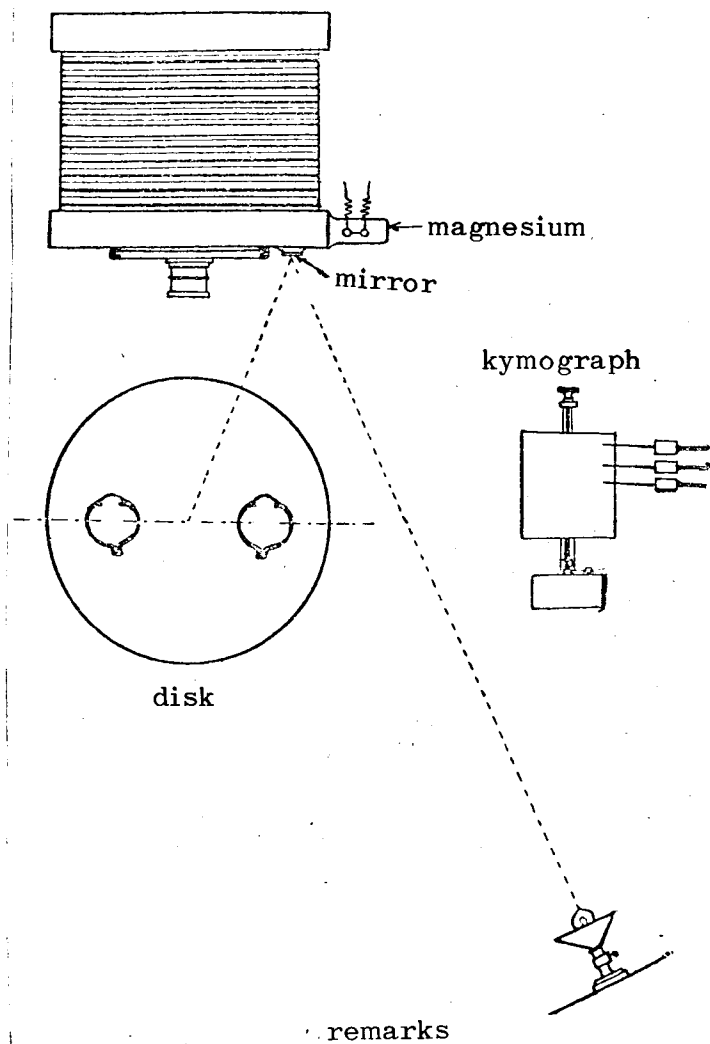


Fig. 7

The lens was located /91 0.75 cm from the eye of the subject and projected an image of natural size on the plate. At the beginning, the turntable was fixed and only a passive head-rotation was carried out, using a cap. The latter had a perpendicular shaft on top, rotating parallel to the shaft of the table. By means of a contact mounted on the cap, two electrical currents were connected in succession; one indicated the beginning of movement when it was opened, while the closing of the second contact caused electrical current to pass through a thin copper wire which in turn ignited the magnesium.

The position of the second contact was selected so that when the current began to flow the head was situated directly in front of the lens during rotation. This meant that the deviation of the position of the eyes was clearly noticeable on the plate.

The axis of rotation of the head was chosen perpendicular to the middle of a line connecting both turning points of the eyes. This turning point, according to Donders and Doyer is located 13.5 mm behind the anterior surface of the cornea.

Hence, each photo could be used for both eyes, if the lens was directed at the axis of rotation of the head.

To ensure that the rotation began with the correct eye position, a mirror was placed in front of the subject at the various

points where the rotation began; a red light hanging 3 m behind the subject was reflected in these mirrors. The eyes were then aimed parallel and straight forward; latent deviations of eye position (heterophoria) were therefore suppressed; the light went out /92 when electrical current was interrupted due to the rotation of the table. Occasionally the light was extinguished by an assistant immediately prior to the start of the motor. This caused no difference. For comparison, we made some pictures in which the subject was looking straight at the camera, and other pictures with deviation of the eye position by 1° , 2° , 3° , 4° , 5° and 6° .

By superimposing these pictures on top of the ones that we wanted to use for measuring the deviation of the eye position, which was very easy because of the sharply defined outer edge of the iris, we could determine the deviation of the eye position for each picture.

The standards were made by locating sights at a distance of 0.75 to 1 m from the subject, on an extension of the beam. The subject could look at them without accommodation and convergence. The interval between the closing of the contact and the ignition of the copper wire and a subsequent interval until the picture was taken was so short that they could be neglected. The ignition time for the magnesium was longer. We checked this by taking some pictures when the circuit was closed to ignite the magnesium, with the subject moving his head as fast as possible. The burning time of the magnesium, however, did make the image on the plate blurred, but the moment at which the current was switched on was clearly indicated in the picture by the position of the head opposite the lens.

The method of experimenting with the cap proved impractical because of the braking of the reflex due to the sensations in the neck. We therefore altered the experiments so as to produce the rotation with the complete table (disk). The contact was now connected to the disk. The other two contacts were also moved. /93

The disk was rotated by a motor just as before, and the recordings were made on a kymograph with two markers, showing the interruption of the current at the beginning of the movement and the connection of a second current to ignite the magnesium.

The reflex time soon turned out to be very short; in order to see a deflection of the eyes with any degree of clarity, the excursion had to have a certain value. It was therefore desirable to use high speeds so that the nystagmus would be proportional to the latter and the eyes would show a noticeable deflection after the beginning of the reflex.

The motor failed us in this respect, as we can see from the following table. The direction of rotation was negative (counterclockwise).

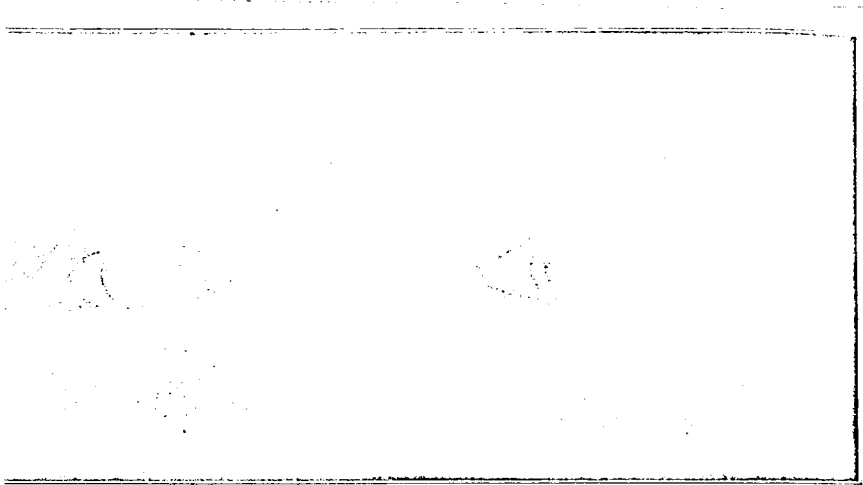
TABLE XIV

subject	accel. (assumed uniform)	duration of rotation in sec.	result		date and number
			right	left	
De G.	12.4	1.7	<i>b</i> 7°	<i>b</i> 6.5°	7 II 2
—	?	1.1	<i>b</i> 5°	<i>b</i> 6°	11 II 4
—	?	0.8	<i>b</i> 5°	<i>b</i> 5°	5
—	?	0.7	2°	2°	6
—	?	0.35	1°	0°	7
					12 II
—	18	1	<i>b</i> 4.5°	<i>b</i> 4.5°	2
—	18	1.1	4°	4°	3
—	16	0.5	4°	4°	4
					13 II
—	7.5	2	5°	5°	5
—	7	1.6	5°	5°	7
—	15	1	4°	4°	8
					15 II
—	13	0.55	4°	4°	1
—	20	0.7	<i>b</i> 4.5°	<i>b</i> 4.5°	2
—	22	0.3	<i>b</i> 1°	<i>b</i> 0°	3
					18 II
—	9.8	0.9	<i>b</i> 6°	<i>b</i> 6°	2
—	25	0.4	4°	4°	3
—	50	0.2	<i>b</i> 3°	<i>b</i> 3°	4
—	19	0.65	<i>b</i> 5.5°	<i>b</i> 5.5°	8
—	20	0.45	4°	4°	9
—	50	0.2	<i>b</i> 1°	<i>b</i> 1°	10

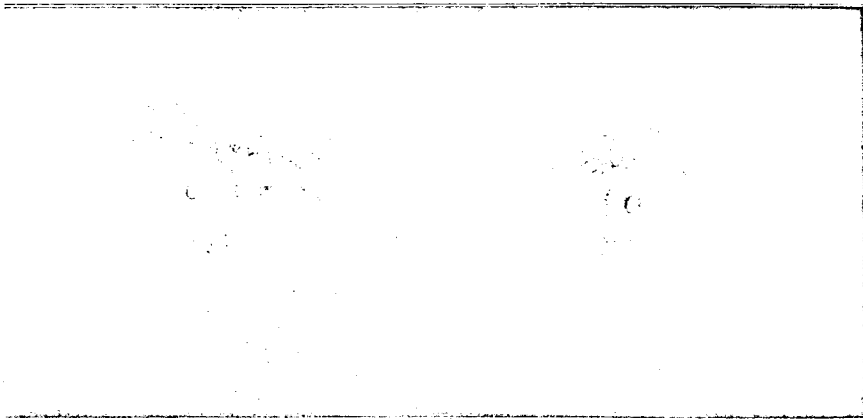
/94

As we can see, the reflex time is not reached at any time, except perhaps at a rotation duration of 0.3 sec (picture 11 II, No. 7 and 15 II No. 3). We attempted to discover whether there was any imperfection in the relationship between the eyes, based on a stronger effect of the labyrinth on the nearer eye. As we can see from the table, the opposite effect is observed.

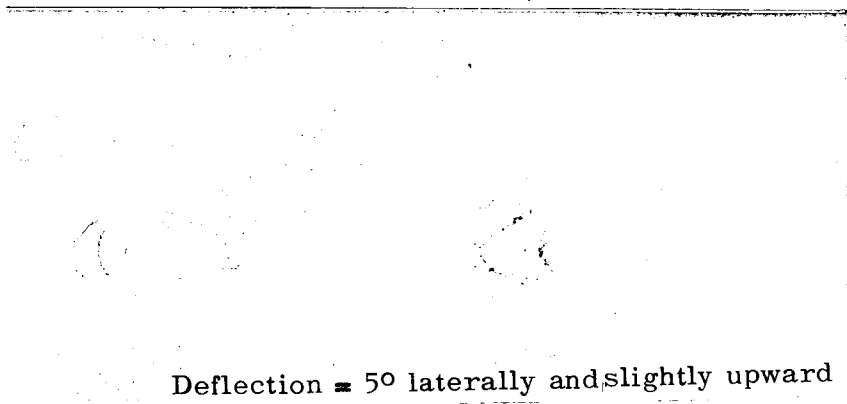
If we agree with Ewald that the left labyrinth is stimulated more during rotation to the left, we would expect the left eye to deflect more, as we find in the case of birds and other animals.



Deflection = 4.5°



Deflection 6.5°



Deflection = 5° laterally and slightly upward

Fig. 8

However, it appeared that occasionally (picture 7 II No. 2, 11 II No. 4) the right eye was displaced further to the right; we also found in certain cases (in which we have added a b to the deflection in degrees) that the eyes were deflected both in the horizontal plane and also in the vertical plane, rather far upward. /95

The amount in degrees of these deflections was never more than 1 or 2.

As an example we have shown some of these pictures in Figure 8.

In order to attain a more rapid rotation of the disk, the motor was replaced by weights.

The rope from which the latter were suspended was connected at one end to the top of the frame, and hung down in a loop, which passed through pulleys both above and below; the other end passed around the wooden disk around which the belt of the motor also passed.

The weights were suspended on a separate pulley, so that they had half the speed of the free end which was passed around the turntable (disk). When the weights were suspended from the rope, the rotation apparatus was fixed in the desired position by a thin, strong cord, connected to the frame and stretched by the pull of the weights.

The apparatus was started by burning or cutting this thin cord. The latter method was better because of the complete darkness which had to be maintained during the rotation.

In this manner, we obtained the following results:

/96

TABLE XV

subject	distance covered	duration of rotation	results		date and number
			right	left	
5 III					
De Gr.	2°	0.15	1°	1°	1
—	2°	0.1	1°	1°	2
—	2°	0.5	< 1°	< 1°	3
—	2°	0.06	< 1°	< 1°	4
9 III					
M.	1°	0.17	0	0	1
—	1°	0.1	0	0	2
—	1°	0.225	0	0	3
10 III					
—	1°	0.16	0	0	1
—	2°	0.3	0	0	2
—	1°	0.25	0	0	3
13 III					

TABLE XV (Continued)

subject	distance covered	duration of rotation	results right	left	date and number
Zw.	1°	0.09	1°	1°	2
					14 III
—	1°	0.12	2°	2°	1
—	1°	0.11	1°	1°	2
—	1°	0.1	< 1°	< 1°	3
—	1°	0.1	1°	1°	4
—	1°	0.11	1°	1°	5
—	1°	0.09	< 1°	< 1°	6
—	1°	0.13	2°	2°	7
—	1°	0.12	2°	2°	8

The difference in the reflex time for subject M is too large to be explained by a repression of the reflex. We very seldom succeeded in obtaining a high speed in this manner; increasing the difference in the speeds of the weights and the disk did not lead to any improvement because of the increase in friction. Therefore, as a last resort we used a very strong, spiral spring as a pulling force instead of the weights. In this manner, rotational speeds were reached at which 1° was often traversed in 0.04 seconds: /97

Gr.	0.06, 0.05; 0.05, 0.04;
Zw.	0.04, 0.05, 0.04, 0.06, 0.06;
M.	0.07, 0.06;

Confusion was caused in this respect by the burning time of the magnesium; the latter was shortened by pre-heating the magnesium and the holder in which it was placed. However with a rotation lasting < 0.06 sec, the picture remained blurred so that it was impossible to see how the eyes were located in their orbits at the beginning of the illumination of the plate. At 0.006 sec and more, a deflection of the eyes from the center was just barely noticeable in most cases.

Returning to the first method of experimentation, i.e., rotating the head alone but now with the hands of the assistant applied flat to both sides of the head, failed to produce any improvement, since the basic cause of the trouble still remained the excessive burning time of the magnesium. Indeed, the periods became shorter:

subject.	duration of rotation through 1°
Zw.	0.03
	0.04
	0.03
de Gr.	0.05
	0.04
	0.04
M.	0.03

However, it could not be determined whether the eyes had moved before the wire burned through.

From these experiments, we can conclude that the reflex time is less than 0.06 seconds.

§3. SENSATIONS

The best way to determine the relationship between stimulus and effect in man is to measure the sensations with several rotations. In these experiments, normal precautions must be taken; the room is illuminated by a light above the subject and the eyes are kept closed and the head fixed. The latter was accomplished with a brace surrounding the face. As a result, the head was bent forward $\pm 25^\circ$, so that the horizontal canal was really horizontal and was the only one stimulated.

a. Minimum Perception.

We began by trying to determine the smallest stimulus which could be perceived. This minimum can generally be reached by decreasing the stimulus with respect to its force or duration. Both methods have been used previously.

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Mach used the torsion of a rope as a mode of force, and measured the duration and maximum acceleration during one period; he determined a minimum sensation with 2° - 3° of acceleration during 14-16 seconds. The stimulus was therefore variable and not uniform.

Delage measured only the final speed, since he considered acceleration to be of lesser importance, and determined the minimum sensation at a final speed of 2° .

Van Rossem had as his objective a momentary stimulus; he succeeded beyond his expectations in limiting the duration to 0.02"; hence, the amount of acceleration had to be large (80°).

To supplement these experiments and by analogy to the reflex experiments, we determined the minimum uniform acceleration which

Would produce a sensation. Then, using the uniform and accurate distribution of the applied force in a given time, we hoped to achieve the smallest possible sensations and stimuli.

It was obvious that in order to obtain a longer, yet very small uniform acceleration, we had to resort to gravity as the mode of force. In the case of our animal experiments, the stimulus had to be too strong and the uniform acceleration was destroyed by the friction of the transmission mechanism. /100

Two weights were attached to either end of a cord which was wound at its center around the wooden disk of the rotation apparatus. Both ends of the cord passed over pulleys, one of which was attached to the floor and the other mounted to meters above it. If one of the weights was now made much heavier than the other, it would accelerate downward, pulling the disk with it. In this manner, we found that a very small acceleration produced no sensation; a somewhat greater acceleration produced a sensation of steady rotation; a still greater acceleration made the subject feel that he was rotating steadily. When the acceleration was increased even beyond the latter point, the subject became aware of the actual situation. This stimulus was then summed and a stronger sensation of rotation was felt. However, one always tends to underestimate the velocity, as we notice when the eyes are open.

The sensation of rotation diminishes rapidly at the beginning of the motion and the repeated acceleration stimulus only establishes the fact that the sensation remains at the same level. The duration of the acceleration was technically limited because the length of the cord and the paths of the weights allowed only two revolutions. Hence, it could not be determined how the sensation might diminish with equal stimulus. According to Mach, this value would eventually reach zero. We did attempt, however, to establish accelerations (and decelerations) by varying the resistance in the electric current, but we were unsuccessful in maintaining this at an equal value per second. A steady motion of the resistance causes increasing acceleration. Only with the method given above and the use of gravity was it possible to give the disk a uniform acceleration. /101

The amount of rotation of the apparatus was recorded by connecting a protruding copper contact to the disk, which would touch four other contacts (all of which were connected to a battery) during the course of one revolution. The electrical circuit was completed through a slip ring; each time the contact on the disk touched one of the four others, a mark was registered on the kymograph.

Using this method, we were able to determine whether the acceleration was uniform, and calculate the values from the elapsed times. If the first revolution time was 15 seconds, for instance, then according to the formula $S = 1/2 at^2$ the acceleration was 3.3° per second. If the acceleration were to remain constant, the sec-

ond revolution time would be 6.6', but it was equal to 9". This was due to the fact that the cords encountered more friction across the pulleys as the weights fell, because the angle of the string to the pulley became sharper as the rate increased. Only the first revolution was valid. The sensation felt during the second revolution was left over from the first and must be considered an illusion because the sound, air flow, slight upward and downward motions, etc., resulting from the already quite high speed informed the subject that he was rotating.

Table XVI below shows the results:

TABLE XVI

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subject.	acceleration	sensation
Zw.	1°;	none
	2° 20';	uniform
	3°;	increasing
v. d. H.	1° 30';	none
	2°;	uniform
	3°;	increasing
M.	1°; 1° 20'; 1° 30'; 1° 30';	none
	1° 30'; 1° 40'; 1° 49'; 1° 45';	uniform
	2° 40'; 2° 35'; 2° 55';	increasing

When the sensations were absent or uniform, the maximum stimuli were measured; for increasing sensation, the minimum stimulus was measured.

The average minimum acceleration of the three subjects was 2° during a reaction time of 0.8 seconds, because in order to know the total amount of the stimulus which produced the minimum sensation, we equated to the product of the force and time as was done earlier during the experiments with the otoliths.

In order to determine the absolute value of the stimulus, we take the measurements of the canals (1.65 cm) and the mass ($m = 0.005 g$) from the calculations of Van Rossem (described on p. 148 of his dissertation). The force (f) then becomes

$$f = m \times a \text{ (acceleration)}$$

a is equal to $2/360 \times 1.65$ cm in linear measure.

$$\text{stimulus } (S) = f \times t \text{ (in dyne-seconds)}$$

$$\text{whence } S = 0.005 \times 2/360 \times 1.65 \times 0.8 = 35.10^{-6}.$$

If we calculate S in the same manner as Van Rossem, then $\alpha =$ /103
 80° and $t = 0.02$ sec. Hence,

$$S = 0.005 \times \frac{80}{360} \times 1.65 \times 0.02 = 35.10^{-6} \text{ dyne-sec.}$$

The brief, strong acceleration described by Van Rossem is therefore equivalent to the weaker one which we applied during the entire length of the reaction time.

Both yield a minimum sensation.

In the case of subject M, the minimum was still lower.

b. Differentiation Threshold.

The following series of experiments was used to measure the differentiation threshold.

The subject was rotated until no further sensations were felt. At this point, the disk was stopped by slowly increasing the resistance to the motor. The resistance was increased so slowly that the retardation remained below the stimulus threshold. The subject was then given a second rotation in the same direction, and had to indicate whether this was faster or slower than the first.

The resistance was calibrated in advance so that a particular speed could be selected which varied from the first as desired.

Table XVII shows the results of these experiments. In this table, we can see the minimum differences in speed at which the subject correctly indicated the relationship between the two values.

TABLE XVII

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subject.	velocity I (in sec of 1 revolution)	velocity II ditto	stimulus difference
R.	280	300	1:15
	168	184	1:10
	80	89	1:10
N.	88	80	1:10
	128	120	1:15
	52	59	1:7.4
M.	48	44	1:11
	180	196	1:11
	20	23	1:7
S.	32	28	1:7
	34	40	1:5.8
	52	60	1:6.5

Subject S is less sensitive, while the others have as their differentiation threshold an average of one-tenth of the stimulus⁵.

c. Merging of Rotation Sensations.

Observations of the summation of sensations within a given sense and the elimination or subtraction of opposing sensations gave us the idea of investigating what would happen when a rotation was periodically interrupted. In order to perform this experiment with the rotation apparatus, we used an upright rod to which a felt-covered cross bar was nailed. This rod was allowed to rotate, with the lower end held in a bearing on the floor and the cross bar pressed against the edge of the disk. The rod was operated manually by an assistant.

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It appeared to be necessary to stop the motor during the periods when the disk was stopped. Otherwise, the transmission ropes would come under too much tension and the disk would begin a new rotation with too great a shock.

Therefore, a small bent piece of rod was attached to the side of the rod away from the disk. The rod was submerged in a mercury-filled test tube standing on the floor, when the felt released the disk. When the cross bar stopped the disk, the rod was pulled out of the mercury, interrupting the current to the motor. The mercury was adjusted so that the circuit was closed and interrupted for equal amounts of time. The disk was rotated at a certain speed (e.g., 24° per sec) and if the duration of the motion and the periods of motionless were varied, three groups of sensations appeared.

I. If the duration of the interruption is long, the actual situation is felt; one feels oneself to be turning and also standing still. When this is analyzed in detail, the following subdivisions are obtained:

Rotation 1.

Increasing sensation of rotation
Maximum sensation of rotation
Decreasing sensation of rotation

Stopping

Increasing after-sensation
Maximum after-sensation
Decreasing after-sensation
Fixed after-sensation

Rotation 2

Increasing sensation of rotation, etc.

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⁵ The duration of the acceleration is about equal for each pair; the equation $v = at$ can be used to calculate the ratios of the accelerations from the final velocities. Among the pairs, t differs strongly.

If the method of starting the disk were completely identical to the method of stopping it, we would have a moment during the rotation in which no motion would be felt. However, the stopping of the disk takes place more suddenly than the start. This means that the after sensation increases more rapidly than the antagonistic sensation and overtakes the former, in other words, a zero point in the oscillation of the sensations is produced when stopping.

II. If the backward and forward motion of the rod is accelerated, the sensations caused by the rotation and the after sensations caused by the stopping merge with one another and the subject feels a backward and forward oscillation around an imaginary point of balance (i.e., rotation and after sensation alternate).

III. With still more rapid motion of the rod, the combination of the three sensations changes once again. They merge and eliminate one another. The subject believes everything to be at rest while he is actually moving in one direction, with short rotational movements alternating with a halt.

The following table gives the durations of the periods of halt and sensations for a given velocity.

avg. speed of turntable = 24°		sensation
(during rotation period)		
duration of periods		
0.44"	standing still	
0.7"	backward and forward	
0.9"	reality	

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This experiment is reminiscent of an analogous action of the sense organs, which appears in periodic stimulation of the retina. If the latter is illuminated with brief interruptions and the field of vision is left black during the pauses, the contrasting impressions fade into one (grey).

Helmholtz [39] divided the surface of the disk into alternate black and white sectors for use in this experiment. If this disk is rotated sufficiently fast, it appears to be grey with a white component equal to the average of all the sectors taken together (Talbot's rule).

In order to be able to equalize the periods, the rod was connected eccentrically to a flywheel; since it was flexible, it moved when pressed against the disk and the periods of standing still and rotating could be kept the same.

In stopping the disk, it moved toward the latter and back again; during rotation the abovementioned contact was immersed in the mercury. It is now possible to determine a period of interruption

which causes fading for each velocity at which the motor starts up sufficiently rapidly.

subject	avg. speed of turntable per sec	interruption period
M	1°	0.60 0.85 0.75
"	2°	0.55 0.52 0.59
"	5°	0.45 0.45 0.45
"	12°	0.44 0.45 0.44
"	24°	0.45 0.44 0.43

The numbers in the first column indicate the average velocities during each rotation period. It would of course have been better to determine the accelerations, but each of these had to be determined individually by recording the motion.

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If we assume the acceleration to have been uniform, then this table can be used for the formula $a = 2m/t$, in which a = acceleration, m = average velocity ($= 1/2 v$) and with conversion of the duration of the periods into the number of interruptions per second (intermission number):

TABLE XVIII

acceleration	intermission No.
3°	1.4
7°	1.81
22°	2.22
55°	2.27
109°	2.27

Therefore, since the stimuli in the sequence nearly double each time, the intermission numbers increase only very slowly. As we have already mentioned in the case of the experiments with frogs, at high velocities the force of the motor is not sufficient so that the acceleration does not increase proportionately at higher final velocities. In view of the larger mass which now had to be moved by the turntable, this drawback was still more noticeable.

However, it is very clear that at higher velocities of the turntable, shorter interruption periods are required. The numbers from which the averages are calculated show less variation at higher velocities; the phenomenon was therefore clearest at a velocity of 24°. The differences in different subjects are sometimes rather considerable. However, a great many other factors are also involved such as the novelty of the sensations, small shocks against the table caused by pressing of the felt, the novelty of having to concentrate one's attention on rotational sensations, and the unpleas-

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ness of the experiment as a whole. We had the opportunity of studying about 20 members of the Dutch Oto-laryngological Association, and found that the sensation of stopping occurred regularly and that in every case a shorter interruption period was needed to accomplish this at higher rotational velocities. Table XVIII is related to us alone.

In the experiments of Helmholtz, the periods of interruption of the white image by the black are 0.04", with illumination of average intensity.

A disk, divided into 6 white sectors and 6 black ones must therefore rotate at least 4 times per second if the production of a grey color is to be complete. If the rotation is slower, flickering appears which means that the individual sectors are not recognized and different kinds of grey are seen, with different ratios of black and white succeeding one another very rapidly.

The intensity of the illumination has an effect on the intermission period required to avoid flickering. The stronger the light, the sooner flickering appears. Photometric methods based on this can be used for white [38] as well as colored [58] light.

Baader [2] made a systematic investigation of how light intensity and interruption time were related, and obtained as a result the following table which can serve as a counterpart of Table XVIII.

light intensity	intermission No. (per sec)
1	19
4	24
18	30
193	41
1800	50

In order to explain the phenomena, we wanted to have an idea of the stimuli to the static organ for at least one velocity. For this purpose, an indicator was connected at one end to the belt which operated the disk; this indicator had a pivot which divided it into two sections with a ratio of 1:4. This horizontal indicator recorded the movement of the table while we were on it, on a horizontally rotating drum. The time was also recorded on the drum in 0.1" intervals; except for the desired control on the action of the braking system, the motion could now be analyzed very accurately and a curve of the acceleration could be derived from the curve on the drum. /110

When the felt is pressed against it, the disk goes back slightly (Fig. 9C) and the after sensation is therefore somewhat strengthened. The periods of rotation and standing still appear to be exactly equal. However, the halting is preceded by a brief period in which the rotation is retarded (Fig. 9B). /111

The abscissa of the motion curve was divided into equal parts; we measured the degree to which the indicator had moved each time

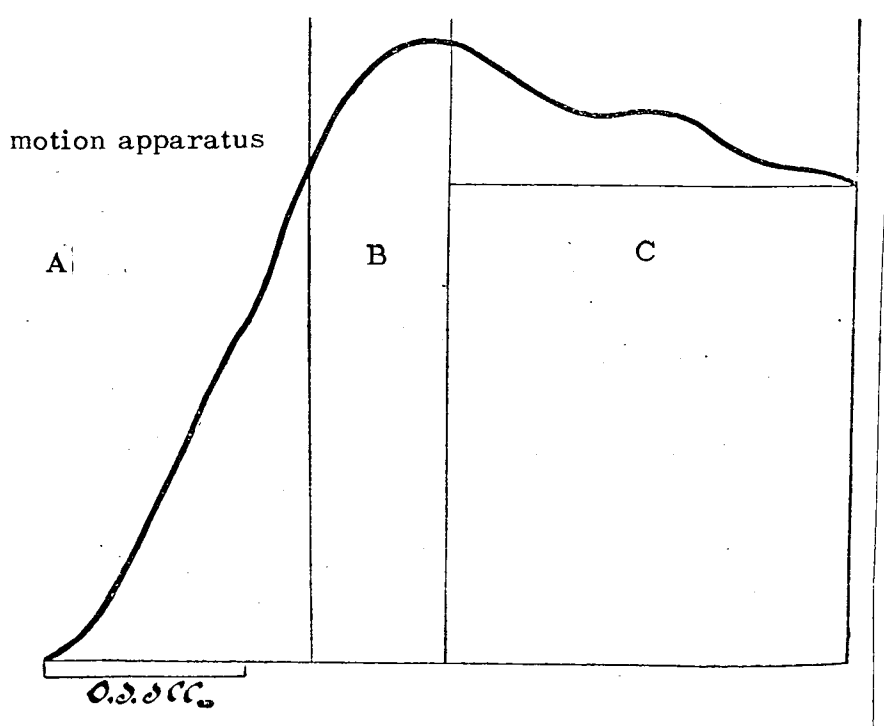


Fig. 9.

in the direction perpendicular to the abscissa. The differences between these sections, when added together, indicated the distance traveled; the differences between these differences showed the (positive or negative) accelerations, and the latter could be plotted as the ordinates of the stimulus curve from which the sensation curve can be obtained. There is no consideration of the fact that the stimulus is a function of acceleration and time, as we did not know how the time influences the acceleration. In general, a greater acceleration naturally requires less time to produce the same sensation.

The circumstances under which the experiment is to be performed are now known exactly and we can attempt to present an explanation.

I. We might imagine that the stimuli in these experiments are below the stimulus threshold because of their short duration.

In order to eliminate this possibility, we made the following test: we recorded the time when the apparatus reached a final velocity of 4° , and the transmission between the electric motor and the turntable could be adjusted so that this time was 0.55". This agrees with the Interruption Test No. 2 from Table XVIII be-

cause if we consider the final velocity to be equal to v and use the normal abbreviations, also assuming the acceleration to be uniform, then for case No. 2, we have /112

$$v = a \quad t = 7 \times 0.55 = \pm 4^\circ.$$

A single one of these rotations is observed very clearly and is appreciably higher than the minimum sensation as far as the senses are concerned. The same was shown to be true for the shorter periods of interruption, for which one might suspect that the decrease in the duration would produce an insufficient sensation regardless of the greater acceleration.

The motion could be regulated so that $v = 5^\circ$ was reached in 0.4"; a is then equal to 12.5° .

This sensation is also very clear; it must produce a fortiori an acceleration of 55° and more, being in force during that time.

It is only with respect to the first combination ($m = 1^\circ$; $a = 3^\circ$; $t = 0.7''$) that any doubt exists that the acceleration is sufficiently large to produce any sensation within such a period.

The final velocity was then attained at a higher acceleration ($\pm 40^\circ$), so that we could not perform the control experiments for this combination. In view of the minimum 2° acceleration discovered earlier, which is in force for at least 0.8 sec, it is better to exclude No. 1 in Table XVIII from further discussion.

II. In addition, fatigue produced by too strong a stimulus of the labyrinth could be an explanation. It is true that the experiment is very tiring and that threshold determinations performed later show important deviations; on the other hand, fatigue would not appear so abruptly and it would be expected that the subject would feel something of the first two stimuli.

In addition, the inaccuracy of such a statement can be proved /113 by a very simple variation of the experiment as follows: after having performed the interruptions for some time, the stick and felt are held back at the moment they are freed from the disk thus permitting this subject to continue rotating. The cords were adjusted in such a way that the final velocity was attained in a period equal to that of the interruption period. The last rotation is then clearly felt.

III. In his first dissertation, Mach pointed out that the rotation sensations in one plane for the two directions can be related as positive and negative, and can therefore eliminate one another. We feel that it can be concluded from this experiment that the same can occur below the stimulus threshold. A sensation is not obtained even if every stimulus alone were sufficient to cause one.

The reaction time for a rotational stimulus is long (according to Van Rossem, ± 0.8 sec) and the interruption period in our experiments was never longer than 0.55 sec. Hence, before one stimulus has the opportunity to be detected by the consciousness, a second has already appeared opposite to the first, and apparently prevents detection of the first. When the interruption period is made longer, e.g., as in the combination on page 69:

$$\alpha = 68^\circ \quad t = 0.7''.$$

The sensation of oscillation then appears.

Hence, a positive stimulus (assumed to be in the direction of rotation) has already produced a sensation before the negative one following it has become sufficiently strong to prevent it. The combination of the two stimuli can serve only to weaken their mutual effect. /114

The explanation of the optical illusion of Helmholtz, more extensively formulated and graphically demonstrated by Fick [27, 28], amounts to the same thing. The impression of light does not reach its maximum immediately. If the section producing this impression rotates, its leading edge (in the direction of rotation) will not be completely sharp, since it has already moved before it is seen with maximum clarity. If the impression has already reached a certain level and is therefore interrupted by the next sector, the decrease will also be smooth although rather steep immediately after the stimulus ends. In other words, the trailing edge of the sector will also be blurred; the white coloring of one will blend with the black coloring of the next.

The discussion becomes much clearer with a graphical representation of the static stimuli and their effects. This has been attempted in Figure 10. Below the abscissa, indicating the duration (time), we have listed the accelerations (as black blocks), each 0.4" long, as well as the corresponding sensations. Above 0.8", these exceed the threshold of the consciousness (line B), reach a maximum after 1 sec, and then slowly decrease until the threshold is reached again after 90 sec. The shape of these curves is based on experiments which will be discussed later on. For their explanation, it is sufficient to mention that the duration of the stimulus is 0.4 sec and the reaction time is 0.8 sec.

Above the zero line, the deceleration stimuli with their sensations are shown. These are in complete agreement with the acceleration stimuli, but are negative with respect to them.

If we now use measurement and subtraction to calculate the resultant of both groups of sensations for different moments and connect the plotted points, we obtain a zig-zag line which runs between the zero line and the consciousness level without ever exceeding the latter. The entire process therefore remains an uncon- /115

scious one; the subject has the impression of standing still. The primary effect of the test was to make it possible to continue the stimulation process after the stimulus had passed; it was only because of this that an opposite stimulus can suppress a given stimulus before anything is sensed.

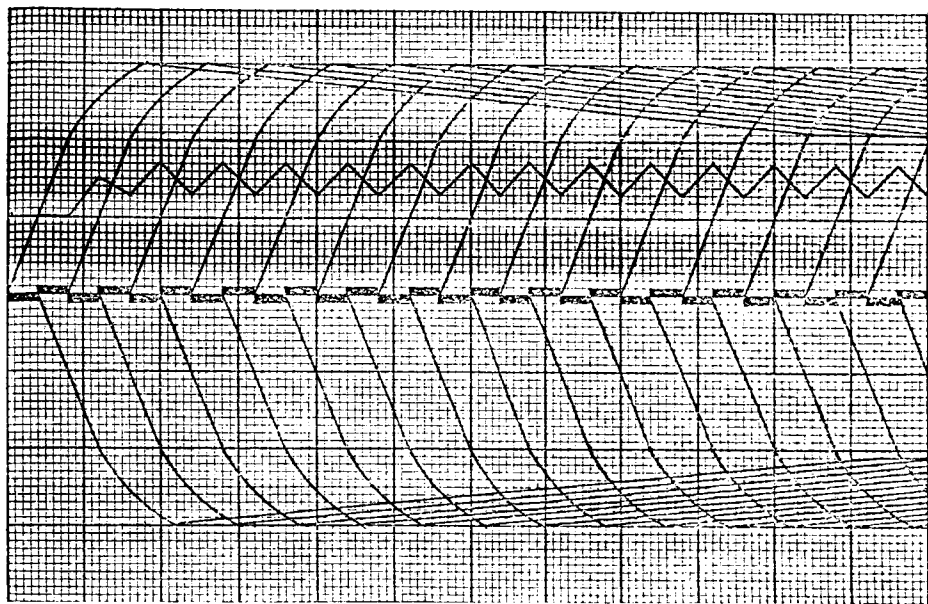


Fig. 10.

In this respect, the experiment can be compared with one by Exner in vision, based on suppression of the positive afterimage. He begins by producing a very short, weak light stimulus which can barely be detected. He then produces the same stimulus, but followed immediately by a stronger one. This has the effect that only the second is noticed. A positive after-effect apparently occurs after the first, weaker stimulus. The period of the positive after-image is very short for the retina, however. Something else must be involved in order to make merging possible. In this regard, we should mention the graph which Fick made for Helmholtz's experiment. In this graph, he showed how a stimulation condition first increases and then decreases when the stimulus is discontinued, then increases again, etc., until a balance is reached. The decrease during the pause is as strong as the increase during the stimulus, so that the impression is one of uniformity. This balance is obtained because the stimulus condition at the start begins more steeply than later.

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This is the critical point with respect to the retina. Hence, Fick was able to derive from the intermission experiment, a curve describing the course of the stimulus condition of the retina.

With Figure 10 in mind, it is very easy to imagine how lengthening the stimulus period can raise the peaks of the resultant curve higher above the abscissa, since the observation process can now continue further. Finally, both lines B will be exceeded. This produces the sensation of oscillation, with alternation of positive and negative sensations. It is also clear that the more steeply the curve rises, the shorter the interruption time must be to prevent this. The location of the maximum will be determined later on for two accelerations. Here we found that the curve rises more steeply with increased acceleration; hence, Figure 10 can now be used to explain Table XVIII.

The same is true for Baarder's table, which was given as a counterpart. If, in the optical experiment, the deviation of the increase and decrease of the sensation remains below the differentiation threshold for a stimulus of that strength, then the impression is uniform. If the differentiation threshold is exceeded, the impression of flickering is produced. The threshold can be exceeded in the same way as in the static experiment, either by lengthening the periods or by strengthening the stimulus.

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The differentiation threshold increases with the stimulus (Weber's law), but the increase in the steepness of the curve is apparently still greater. The latter, as well as the ratio according to Weber's law, are the basis for the relationship between the numbers in the two columns of Baarder's table.

The necessity of making the periods (of rotation and standing still) smaller at higher accelerations can also be explained, because the reaction times are then shorter (as was previously pointed out by Van Rossem); they are not much shorter.

In order to do an experiment on the labyrinth which is completely analogous to the retina experiment is not very feasible from the technical point of view. We attempted to use a rheostat to vary the resistance and thereby obtain successively increasing accelerations at uniform velocity. The latter were supposed to produce a smooth sensation of rotation of a sufficiently short duration. However, the velocity then increases too rapidly.

In summary, we can see the following facts by comparing the static experiment with that of Helmholtz:

(a) the following observations are in agreement for the two experiments:

(1) merging of periodic, contrasting sensory stimuli;

(2) an intermission number which is a function of the strength of the stimulus;

(3) sensation of flickering or oscillation with extension of the periods.

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(b) The experiments differ in the following respects:

(1) in the retina, everything is above the stimulus threshold, while for the labyrinth everything is below it;

(2) the differentiation threshold for the retina is exceeded in Case 3, while the stimulation threshold is exceeded for the labyrinth;

(3) the period for the retina is $\pm 0.04''$, for the labyrinth it is $\pm 0.4''$;

(4) merging takes place for the retina, while subtraction of both processes is involved in the labyrinth.

d. Progress of the Sensation.

We have attempted to trace the portion above the stimulus threshold by measuring the stimuli capable of eliminating the sensations in different phases of their existence, in connection with a study of the progress of the stimulating condition in the labyrinth, to the extent that this remains below the stimulation threshold and can therefore not be recorded experimentally.

We did not succeed with the first part of the sensation and could determine only indirectly where the maximum was located. The manner in which the elimination was achieved technically will be discussed later on; the results will also be given. At the same time, it will be apparent why this method led me astray with respect to the beginning of the curve. To determine the moment at which the sensation was strongest, we had to find a different combination of stimuli and therefore happened upon the following experiment: /119

To begin with, the subject is rotated until no further rotation is sensed; then the actual experiment begins, consisting of three parts as follows.

1. Stopping and remaining still for a brief moment.

2. Renewed rotation at the same velocity but in the opposite direction, for a period of time as short as in 1 above.

3. Reversal of rotation, with maintenance of the same speed.

The result is that reversal is sensed as disappearance of all sensations at certain ratios between the rotation velocity and the periods.

This result can only be obtained when the sensations produced by the motion described in No. 1 above as well as those in No. 2 have reached maxima before they are respectively strengthened and

interrupted by the next stimulus. Motion No. 3 combines Nos. 1 and 2, but it is in the opposite direction and can only occur when the other two have completely finished; hence, if one of the preceding sensations had already been strengthened or interrupted before its maximum, complete elimination could never occur with reversal and only rotation in the direction prior to motion No. 1 would be sensed.

It does not matter who is seated on the turntable because the same type of movement which is involved in Nos. 1 and 2 must also be felt in No. 3.

In order to make this experiment technically feasible and to /120 record the duration of the movements and the pauses, a setup was arranged in the room adjacent to the motor, which could be controlled from the turntable by the subject.

By using slip rings under the turntable, it was possible to transmit two currents to two switches, which were mounted in front of the subject and could be operated by him. Both currents were grounded through the frame.

One was the current for the electric motor; the seated subject could therefore cause himself to rotate.

The second current was also led to the adjacent room and passed through an electromagnet (see Fig. 11); the latter served as the winding of a relay, and when the circuit was closed it switched the connections to the motor terminals.

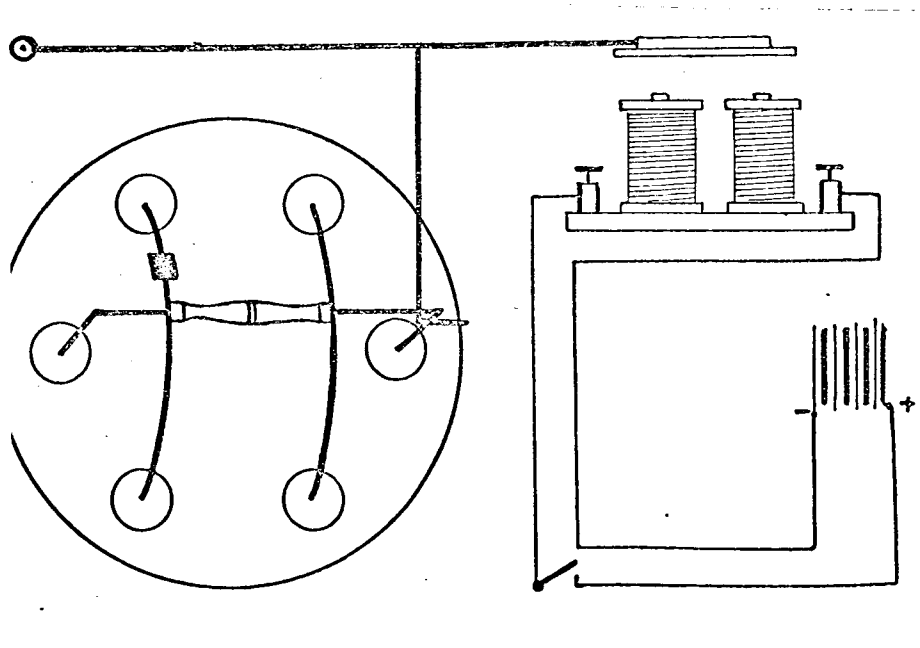


Fig. 11.

If the current through the electromagnet was interrupted, the relay returned to the original position by the action of a weight and the motor turned in the previous direction. In this manner, the subject (seated on the turntable) could suddenly reverse the motion of the latter. In addition, both circuits included signal markers writing on a kymograph, so that the opening and closing of the circuits could be recorded in addition to the time, as marked at 0.1" intervals by a time marker. /121

Finally, we could also use a wire (led through a hole in the wall) to start the kymograph from the table when the preliminary rotation had lasted long enough. In this way, we could first determine on ourselves when elimination was obtained at different velocities in order to subject others to the same movements from the adjacent room later on and compare the results.

At first we did not know exactly where the maximum of the stimulus was located on the basis of these experiments. We therefore simply assumed the moment at which it began (actually, it occurs only slightly afterwards at $\pm 0.1''$). This is due to the friction between the parts of the shaft in contact, which must first be overcome. Acceleration increases later because of increased friction. Due to the complex transmission, this increase was appreciable with every increase in velocity.

If we can measure the recording described above and thus determine how long the table was at rest (measured from the beginning of braking) and how long the second rotation lasted (also measured from its beginning), then we can determine the duration of the increasing portion of the sensation by subtracting the reaction period.

We assumed the reaction period to be 0.8", ignoring the small differences with different velocities.

TABLE XVII*

subject	velocity	duration of standstill	duration of rotation II
M. C.	15°	2"	1.25"
—	15°	2.25"	1.5"
N.	15°	2"	1.5"
Z.	35°	1.5"	1.5"
Z.	15°	2"	2"
M.	35°	1.5"	1.5"
—	35°	1.5"	1.5"
—	—	1.5"	1"

*Translator's Comment: There are two Table XVII. /122

TABLE XVII (Continued)

subject	velocity	duration of standstill	duration of rotation II
—	15°	2.5"	2.5"
—	15°	1.5"	1.5"
—	15°	1.5'	1.5"
R.	15°	2"	2.25"
R.	15°	2"	2.25"
v. d. M.	35°	1"	1.25"

averages for the 6 subjects:

velocity	standstill	rotation
15°	1.9"	1.8"
35°	1.3"	1.3"

or, with subtraction of the reaction period⁶

15°	1.1"	1"
35°	0.5"	0.5"

/123

The position of the cord was adjusted so that the accelerations were proportioned as 1:2 at final velocities of 15° and 35° (at least at the beginning).

The velocity was then $\pm 10^\circ$ one second after the start at final velocity 15°, so that the acceleration was $\pm 10^\circ$, and with a final velocity of 35° it was $\pm 20^\circ$ at that time so that the acceleration was $\pm 20^\circ$. We have ignored the influence of the acceleration, persisting after the reaction period, on the increase of the sensation.

It is very clear that the acceleration and deceleration increase as the sensation reaches its maximum sooner. However, there is also a small distinction between the increase in the sensation of stopping and that of the second rotation. This is because the stopping occurs somewhat less suddenly than the start.

We attempted to correct this by placing a brush against the wheel of the motor; although this also retards attainment of final velocity, a brake of this kind can be adjusted so that the differ-

⁶We performed some experiments in increasing acceleration by changing the resistance, and could see that each increase had its own reaction period. This must then be subtracted for each subject individually.

ence between the two stimuli can be reduced appreciably. Nevertheless, a difference still remained, so that regardless of the equal terminal and initial velocities for rotation and stopping, the maximum sensation in rotation was reached somewhat earlier. If the stimulus is divided in such a way that it first increases sharply and then decreases rapidly, and then increases more slowly and then decreases slowly, a higher maximum sensation can be obtained in the first manner at a moment sooner after the start, with all of the stimuli being completely equal. /124

It would have been desirable to obtain additional velocities, but then the motor initially produced two few velocity differences. Therefore, the higher and lower velocities were obtained during longer and shorter periods, respectively. The stimulus changes its duration only, but does not show sufficient difference in the degree of sensation.

Otherwise, if the same relationship existed here as Exner found for light, we could have determined that a geometrical increase of the stimulus causes an arithmetic decrease of the periods of the maximum. We would then have used a spring as the mode of force, just as we did earlier on the small turntable for animals. The descending part of the curve is easy to follow in its course. The method which we used was also based on the elimination of the sensation by a new opposite stimulus; the second is now weaker than the first.

We chose the moment of its application so that the maximum came at the height of a decreasing after-sensation.

Since we know the position of that maximum with respect to the starting point from the last experiments, the point on the curve of the after-sensations can be determined each time. This coincidence of the maximum of the weaker sensation with the decrease of the first one is sensed as elimination. This elimination in itself lasts some time; after describing the experiment, we will return to this topic. /125

Since these values were obtained in each case with small differences in acceleration at different motor speeds, and we could not be absolutely sure that the stimulus was the same in each case, we decided to use as the target of myour investigation the course of the after-sensation during stopping. It was now essential to use a method of stopping which would ensure that the same person with the same velocity would also always stop at the same rate of deceleration. In order to be independent of the motor, the current to the latter was interrupted before stopping and the disk was stopped in the same way that was used for the large kymograph of Engelmann, a description of which can be found in the thesis by Dr. W. A. Boekelman (Utrecht, 1894).

The latch with the two cross springs was connected to the top

on the shaft with the disk, and the fixed springs were connected to the frame. These could be moved so that the latch could move past undisturbed. If it was desired to stop the turntable, the springs were moved until they engaged a stopping mechanism and the latch passed between them, stopping the apparatus. The action of the latch passing between the springs separated the latter and also compressed a coil spring, which could be adjusted so that the stopping arrangement could be regulated for operation at different velocities. Stopping occurred very smoothly and could be recorded very accurately. A pointer about 40 cm long was connected to the metal disk. /126

A kymograph was mounted with its shaft horizontal and parallel to an imaginary tangent to the disk; the pointer recorded a curve on it. The position of the kymograph was chosen so that the pointer wrote on it only during the stopping process and remained in contact with it when the disk stopped.

For recording, the subject whose after-sensations we wanted to measure later on took his position on the disk. The pointer recorded a curve on the rotating kymograph, and we could measure the course of the acceleration by comparing this curve with those made with a rotating disk and a standing drum (1) and a rotating disk and a rotating drum (2).

The time was also recorded at 0.1 sec intervals during all the recordings.

Measurement proceeded as follows. We will refer to the curve produced during stopping as 3. The pointer now makes three motions:

- a. Tangential, with uniform velocity;
- b. Centripetal, and accelerated;
- c. Rotation produced by turning of the kymograph, perpendicular to the shaft of the latter and counter to its rotation.

It is sufficient to know a ; we therefore eliminated the curvature by subtracting Curve 1 from Curve 3 to produce 3'. By comparing 3' and 2, we could see where the stopping began (i.e., where the curves were no longer parallel), and how long this condition lasted (by examining time markings).

Now, by plotting an abscissa as an extension of the line after stopping and comparing the perpendiculars dropped to it from Curve 3' according to the time divisions, we obtained the distances covered in those units of time; from this we were able to determine the velocities, and from the differences in the latter, the deceleration (i.e., the stimulus). /127

Figure 12 shows the course of these decelerations.

In the first place, the curve appears to be very smooth; it

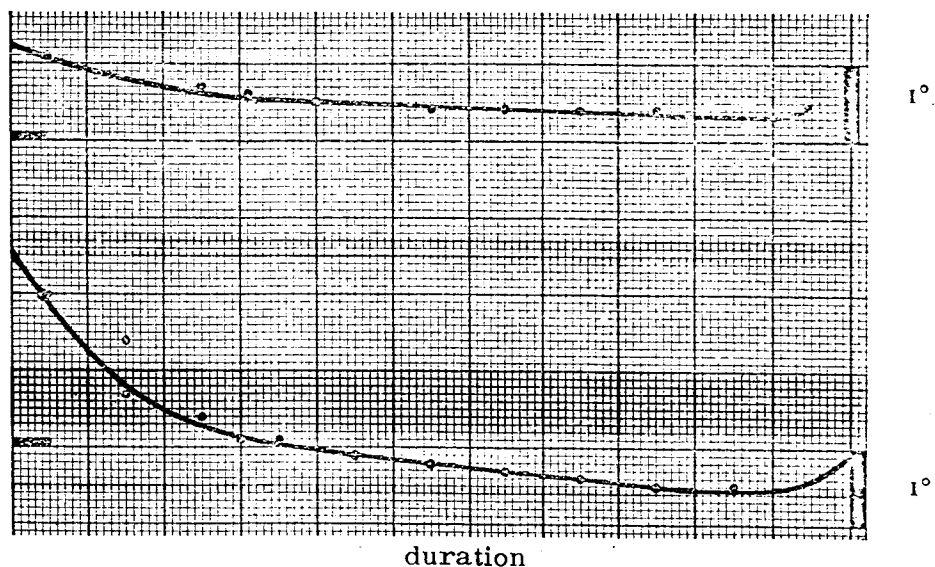


Fig. 12

also has the same appearance in successive recordings. The stopping was not uniformly decelerated, since both the tension of the springs and friction were involved. The deceleration decreased very strongly at first (0.3") but became rather uniform above velocity 24° (lower curve) and remained uniform thereafter except at the very end. At the beginning, owing to the considerable friction between the springs of the latch and the other two springs and the considerable increase in friction when the disk was almost at a standstill, these deviations from uniformity are clearly explained. /128

Above a velocity of 12° , the deceleration initially decreased somewhat (0.2") and remained uniform from then on except at the very end. The duration of the deceleration was 2.1 sec for a velocity of 12° and 2.2 sec for a velocity of 24° . It would perhaps have been better to use instead of this spring mechanism and its friction problems a coil spring like that used earlier for the small turntable (in the animal experiments). The tension of the brake mechanism could then have prevented that problem with rotation of the table or disk.

The ratio between the stimulus and sensation was now too complicated at the velocity of 24° in order to be understood completely.

The stopping mechanism was now satisfactory, but elimination required rotation in the direction of the first rotation so that the same difficulty was encountered with respect to starting the motor. This drawback was overcome only by rotating the head in an axis parallel to that of the table. In order to be completely sure regarding the latter and to be able to perform the rotation

passively, a cap with a rotatable top was connected to the frame. An electric motor with a rheostat was mounted on the large apparatus. This motor transmitted its motion to the cap and thus to the head.

Parallel to **the shaft of** the table, there was a second shaft /129
free to rotate at top and bottom in holes in boards screwed horizontally to the frame and extending as far as the steel supporting poles around the table would allow. A piece of felt which extended below the lower board operated a switch connected to the motor circuit; this switch, mounted in a holder nailed to the floor, was operated just before stopping. This therefore ensured that the current was interrupted always at the same moment before stopping.

Disks were connected above and below this secondary shaft. The motion of the motor was first transmitted to the lower disk and then through the shaft to the upper disk, and further by an intermediate disk to the cap. The latter was accomplished with a silk thread which passed around the transmission shaft on one side, then through a holder which kept it under tension with respect to the transmission, and then to the cap, where it was wrapped around a disk on top of the latter. If the motor were started, the thread was tightened, and when the motor reached full speed (at high velocity) the cap and the subject's head were suddenly turned.

Transmissions with gear reduction have the advantage that the motor can turn rapidly (and therefore smoothly), while the head was moved only slowly but did not affect the speed of the motor at all despite its resistance. Since the silk thread is first put under tension when the motor is at full speed, the stimulus becomes short and uniform for a given adjustment of the motor speed. When measuring the movement curve, it was found that the angular acceleration of the head lasted for a maximum of 0.02 sec.

The recording was done in the same manner, i.e., by connecting an indicator to the cap and permitting it to record its motion on a horizontal rotating kymograph. /130

Instead of an electric mode of force, it might perhaps have been better to use a coil spring for moving the head; however, this is difficult to achieve in practice.

We must now proceed to a description of the recording of the experiment.

The velocity of the turntable was determined with a stopwatch.

At the same time that the switch operating the motor current was turned on, the abovementioned piece of felt operated a second switch to interrupt the current to a signal marker. On top of the cap, there was a contact which touched a second contact, insulated

from the frame, when at rest. As soon as the head was turned, this circuit was broken and also indicated by another signal marker. Both signals were recorded on the kymograph. The movement of the cap was also measured with a stopwatch.

Before continuing with the results of the determinations, we should like to review whether there might still be some errors in this method.

1. It might be possible that the cap would turn eccentrically with respect to the turntable shaft on an axis parallel to the other. This did not have to be taken into account (see Van Rossem's thesis, p. 113), since we could easily ascertain ourselves that turning of the head with the cap (actively or passively with the motor) during rotation, when the sensation of the latter had disappeared, caused absolutely no new observation of rotation, just as when the head is turned in a plane other than the horizontal; on the contrary, if one still had a sensation or after-sensation, then a slight turning of the head with the cap was sufficient to eliminate this or to strengthen it, depending on the direction chosen. /131

2. It might be possible that the head turned inside the cap when the silk thread was pulled.

Hence, two vertical lines were drawn on the forehead, in line with one another. These lines did not shift with respect to one another.

It was therefore certain that in the experiments, no additional rotational stimulus was added to the original one other than those which were directly opposite to the first and could be measured by the amount of turning of the cap.

3. However, a real drawback was that in the first rotation only the static organ was affected; the motion of the head, however, added the sensation in the atlanto-epistropheus joint, which reinforced the second sensation.

The result was the following: regardless of that reinforcement, when the second stimulus was kept weaker than the first, it was possible to have a simultaneous sensation of rotation to the left and right in the neck, resembling the after-sensations in the labyrinth. This could be overcome only with practice ⁷.

4. We should like to deal with still another, final drawback, which we mentioned earlier; namely, that the elimination itself requires some time. One can feel the competition between the two /132

⁷ An important point in this test was expert assistance, if we wish to avoid being restricted completely to the observation of our own sensations. We had the opportunity to avail ourselves of such qualified assistance.

sensations and is uncertain for a few moments which rotation direction is the dominant sensation until everything disappears rapidly and only the sensation in the neck remains. This period of merging is $\pm 0.2''$. We attempted to record by making the subject signal at both ends of this period. However, as soon as the subject had to occupy himself with something else, the accurate observation of his sensations was hindered and the result was not clear.

If we can now imagine the graphical representation of the experiment, we will have first the curve of the sensation which at first rises steeply and then descends slowly. The initial rise is not felt very clearly. The second curve of the head movement is not observed at different points.

Everything that happens depends on the strength of the second stimulus. If it is stronger, it eliminates the first sensation and continues to exist in a weakened form.

If it is of the same strength, then all sensations will disappear and the curves will have one point in common, i.e., a point on the descending after-sensation curve and the high point of the auxiliary curve of the head rotation.

If it is weaker, then the sensation is merely reduced and the two curves do not intersect.

However, the second sensation (just like the first one) will not reach its maximum immediately; the intersection with elimination (i.e., coincidence of that maximum with any point on the first curve) will therefore be to the right of the base point if we imagine the time to be marked on the axis from left to right.

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Maxima were reached earlier after 1 and 0.5 sec, respectively; we used as the values for the time (including the reaction time) 1.8 and 1.3 sec after the beginning of the stopping. Since the stimulus was strongest at the beginning and about the same as that applied at that time, the maximum could be assumed to lie at the same point on the curve. In this experiment, the decelerations were 6° and 11° per sec on the average, being about twice as large at the beginning and therefore about equal to the acceleration in the other experiment. The moment of the beginning of the head motion was recorded; this acceleration stimulus was so short that the motion could be judged from its final velocity only. For determining the intersection of the two curves (the main curve and the auxiliary curve), only the reaction period was used; taking into account the increase of the sensation, we use a liberal value of 1 sec for the latter.

In performing the experiment, we first attempted to determine which combinations of time and velocity would produce elimination and then recorded them on a new recording period. Tiring had a very strong influence. Therefore we only performed a few exper-

ments each afternoon since dulling of the reactions otherwise cause the sensations to disappear too quickly.

Our efforts at compensation failed when we were very close to the maximum. The two sensations created confusion which lasted a rather long time and it could not be determined which of the two was predominant.

The joint sensation in the neck was then disturbed by the faster head rotation.

The following tables indicate the condition for elimination of the sensation for a subject who is not tired. The columns list the following: subject, velocity of head movement, time at which the latter began, counted from the beginning of stopping (in Table XVIII this is for a rotation rate of the disk of 12° , while in Table XIX it is for 24° per second.

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TABLE XVIII*

subject	velocity of head movement	time between start of stopping and start of head movement (in sec)
De Gr.	8°	2.6
—	7.2°	3
—	6°	2.9
—	5°	3.9
—	4.3°	4.7
—	3.2°	6.7
—	2.6°	7.1
—	1.5°	9.1
M.	8°	2.4
—	7.2°	2.4
—	6°	3.1
—	5°	3.5
—	4.3°	4.5
—	3.2°	5.3
—	2.6°	8.3
—	1.5°	9.1

rotation velocity of the disk = 12°

duration of stopping = 2.1 sec; deceleration therefore = $\pm 6^\circ$ per sec

*Translators Comment: There are two Table XVIII.

TABLE XIX

/135

subject	velocity of head movement	time between start of stopping and start of head movement (in sec)
De Gr.	8°	2.2
—	7.2°	2.6
—	6°	3
—	5°	3.4
—	4.3°	3.9
—	3.9°	4.1
—	2.2°	6.2
—	1.5°	14.2
M.	8°	2.2
—	7.2°	2.4
—	6°	3.7
—	5°	4.1
—	4.3°	4.7
—	3.9°	5.2
—	2.2°	10.2
—	1.5°	14.2

rotation velocity of the disk = 24°
duration of stopping = 2.2 sec; deceleration therefore = $\pm 11^{\circ}$ per sec

In summarizing the manner in which a curve was derived from these data, the following facts should be pointed out.

1. The reaction time was taken as 0.8" for all velocities.
2. The time required to reach the maximum was assumed to be 0.2" for the auxiliary curves while 0.5 and 1 sec were used for the main curve (from direct determination).
3. Disregard of the time required for the merging of the sensations.

4. In sketching Figure 10, we observed that the experimentally determined figures mean that the maximum was not located on the extrapolation of the line connecting the beginning of the stimulus with the point at which the threshold is crossed, but below it. The maximum was located on the extrapolation of the original sensation curve, then the result was above the line taken as the conscious level. This was in contradiction to the observation made during the experiment (merging below the threshold). We can therefore conclude from the experiment that the curve has a shape which

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convex upward. The degree of this steepness reduction must therefore be at least 25%, which can be derived by calculation from the figure, with a few small errors. Since in Figure 10 the stimulus time was taken as 0.4 sec instead of 0.44 sec as in the experiment for the sake of convenience, the result did not run immediately below the threshold but was well below it. In the experiment, however, we looked for the longest stimulus period which would still cause merging; this meant that the result came just below the threshold and the curve had a somewhat lesser degree of curvature than in Figure 10. Hence, the sensation curve (Fig. 13) showed a lesser curvature between the origin of the line and the maximum.

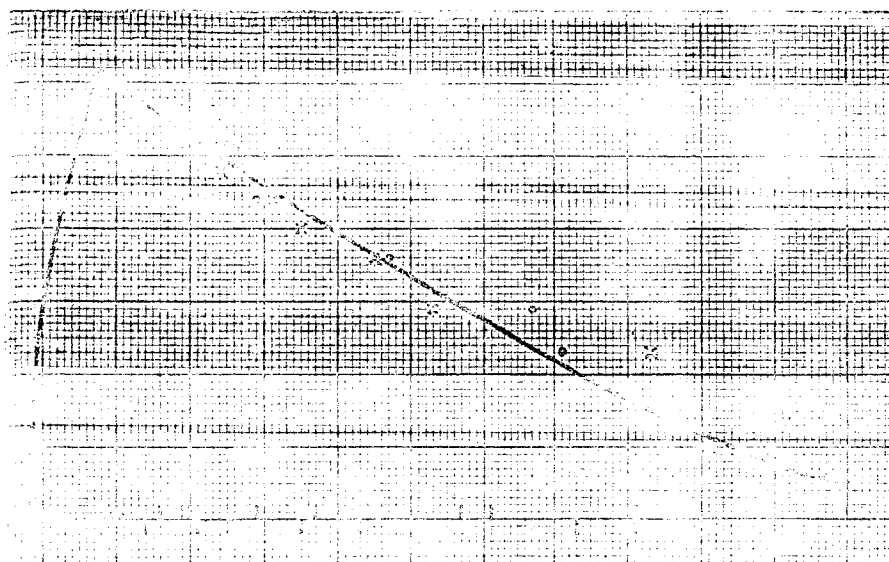
This is a point of agreement with the sensation curve for the retina, with the stimulus similarly interrupted. This was constructed by Fick [27, 28], on the basis of Helmholtz's oscillation experiment, which we have already compared with the static one. He began with what we refer to as the result and derived a curve whose shape showed considerable similarity to the static curve, especially with respect to the initial curvature before the maximum.

The moments of starting of the head movement are once again /138 plotted along the abscissa.

The logarithms of the accelerations are plotted on the ordinate (on the basis of Fechner's law [26]). These accelerations are proportional to the final velocities, since the stimulus was always assumed to be of equal duration (± 0.02 sec). Here, the natural logarithm of the final velocity 1.5° is used as unity, since it represents the threshold approximately.

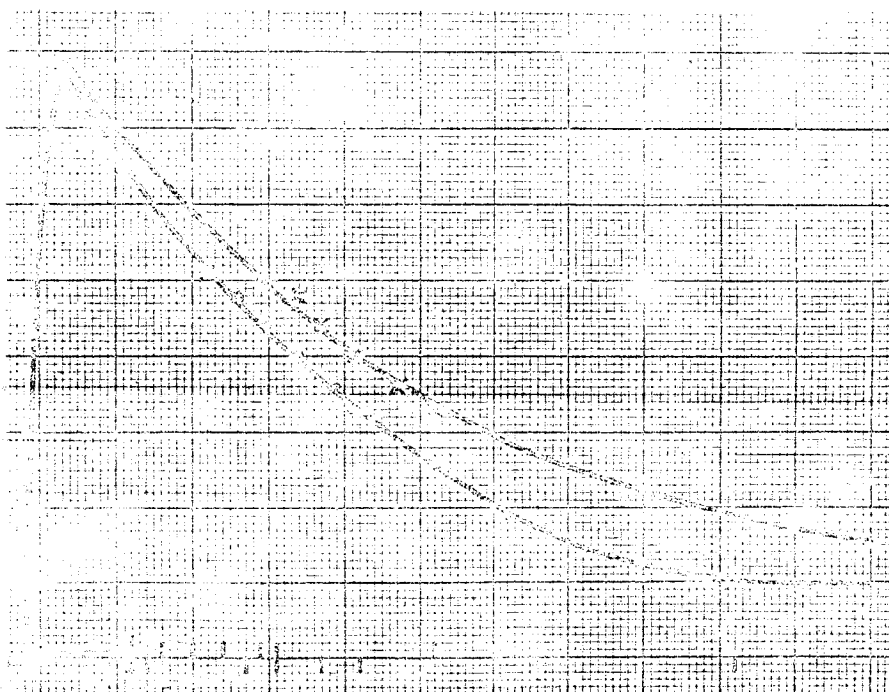
Therefore, both curves in Figure 13 are derived from Tables XVIII and XIX. For the lower curves, the last of the points determined falls outside the graph.

In order to understand the curves completely, it is also desirable to compare them with those in Figure 12, which represents both stimuli causing the sensations.



rotational
velocity
120° per sec

1 sec.



rotational
velocity
240° per sec

1 sec.

• = De Gr. x = M

Fig. 13.

SUMMARY

A brief summary of the results obtained follows.

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Part I. OTOLITHS.

For this organ, we conducted two groups of studies with the guinea pig, which concerned the reflex time and the most advantageous administration of the stimulus in the case of a vertical motion. This reflex time was found to be about 0.12 sec. No noticeable difference in time was found for highly divergent accelerations.

The minimum required stimulus could best be determined by uniform acceleration. In this case, the motion was controlled pneumatically.

At first, the mode of force was uniform, then decreased suddenly because of the increase in velocity and finally provided only a uniform velocity. Hence, the acceleration was uniform at first and zero afterward.

It appeared that a minimum reflex motion could be produced by very different degrees of stimulation. This amount was calculated from the duration and magnitude of the acceleration.

By far the most economical method of administration was that employing a uniform stimulus divided over the reflex time; shortening of the duration of the stimulus can result in an 18-fold loss. /140

Part II. SEMICIRCULAR CANALS.

§ 1. *Reflexes.*

The various reflexes were generated at the following reflex times:

subject	reflex	stimulus	reflex time (in sec)
pike	eye movement	electric	0.15
frog	head rotation	rotation	0.3
turtle	" "	"	0.27
guinea pig	" "	"	0.2
man	eye movement	"	<0.06

It was necessary to operate on the pike in order to reach the organ and be as certain as possible that it was mainly the horizontal canal which was stimulated. In the case of the other animals and man, this was taken for granted on the basis of the experiments mentioned in the literature summary.

In the pike, frog, turtle and guinea pig, the reflex could be recorded directly. We photographed the eye movement in human subjects, but were unable to determine a smaller duration than 0.06 sec because of technical difficulties. While the reflex times of animals show little difference and also do not show much deviation relative to the otolith organ, the reflex time in man is much shorter and (what is more important) much shorter than the reaction time (0.08 sec). This alone should suffice to indicate that the rotation sensation may be nothing more than a sensing of the reflex; in that case, however, the latent period of this feeling (0.8 to <0.06 = at least 0.7 sec) is very long; in addition, the uniform course of the sensation makes it unlikely that a harmonic oscillating reflex such as nystagmus would be the cause of the latter. The frog turned out to be best suited for a total analysis of head motion. As the peculiarities of this movement were only significant when the cause of stimulus was known exactly, uniform accelerations were used. The results initially seem to indicate more of an analogous relationship between the stimulus and reflex than between the latter and the static sensation, thus satisfying Weber's law. /141

A closer comparison of an increasing series of stimuli with the head motions generated by them showed that the speed of the latter movement is directly proportional to the intensity of the stimulus.

If the acceleration reaches higher values (38° per sec), different frogs show individual values which are so different that no usable averages can be obtained; this means that the reflex is close to its maximum activity (reflex intensity).

§ 2. Sensations.

In accordance with the results from the otolith experiments, we attempted to determine the minimum of stimulus which would still cause a sensation by distributing the acceleration equally over the entire reaction time. The amount of stimulus was expressed

by the product of the force and time of application. Calculated in this manner, the stimulus was as great as the momentary one applied by Van Rossem.

The minimum increase in stimulus that could still be felt appeared to have a regular uniform relationship to the degree of the stimulus, as is the case for most organs (Weber's law); in this case, the ratio was 11 to 100.

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Periodic administration of alternating rotational stimuli in opposite directions could produce a merging of their effects by proper selection of the quantitative ratios. The merger occurred below the consciousness level, analogously to the familiar merger above it, when rotation was stopped but the subject could still feel it. Increased acceleration called for a shortening of the period if the merger were to be complete. If these quantitative stipulations were not satisfied, a feeling of oscillation resulted; we were therefore led to compare the static phenomena with familiar optical ones.

In order to be able to represent graphically the sensations stimulated by this experiment, we required more facts at our disposal regarding its course. We attempted to construct a complete curve of the sensation as follows. We began with two known stimuli (always stopping in the same manner after certain velocities).

We knew the reaction time as well as the duration of the sensation, which could be determined directly.

First of all, we looked for the position of the maximum. In accordance with the ratio of the acceleration and period of interruption in the merger experiment, we found that at higher accelerations a maximum of this kind was reached earlier. There still remain the rising and ascending parts of the curve between the three known points (exceeding of the stimulus threshold, attainment of the maximum, and disappearance of the latter). We found a few points in the ascending portion by stimulating counter sensations, which we were used in the graphs as auxiliary curves whose maxima always coincided with a point on the desired curve. This was interpreted as elimination of the sensation.

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This method failed immediately before and after the maximum. The graphical representation of the merger experiment showed that the curve before the maximum must exhibit a decrease in steepness. It is only then beginning with the numbers determined empirically, that the resultant of the two groups of sensations remains below the threshold, as appeared to be the case on the basis of observation. This decrease had to be at least 25%. This meant that virtually all of the curve was known. The graphic representation expressed the strength of the sensation as the logarithm of the stimulus causing it or, in case it was opposite, the logarithm of the stimulus eliminating it, with the stimulus threshold taken as unity.

POSTSCRIPT

The Static Organ and Games Involving Motion.

In discussing games, it seems practical to begin by dividing them according to the motives involved. However, there are so many different factors which stimulate man and the animals to play games that this soon turns out to be impossible. The desire to move, pleasure in displaying and excelling in dexterity, social motivations, and stimuli of distinct sensations in the player or spectators; all of these factors exert their influence, to varying degrees. In this way, we can discuss a wide variety of different games. /144

Various classifications also have another effect, that of developing a precise order for the games.

Carl Groos [35, 36] divides human games according to the organs involved. He uses a broad interpretation of the idea of "games", but does not name even one which could be related to the static organ. He lists all the games which he considered under the heading of "motion games", subdivided into two groups: passive and active.

His summary follows (with some modifications and additions): /145

I. Passive.

Swinging (swing, rocking horse, hammock), rocking, see-sawing, riding a merry-go-round, riding (horseback, roller coaster), sailing, sleighing (tobogganing), high diving.

II. Active.

Dancing, skating, jumping, walking on stilts, skiing and walking-the-beam.

If we compare his classification with the function of the static organ, we see immediately that the various activities of this sense organ are completely reflected in this system.

The passive games are based on sensations involving stimulus of the semicircular canals, otoliths (see-sawing) or, most of all, a combination of both (typical of swinging).

Active games are directly associated with the labyrinth reflexes, especially those which serve to control balance. There is no strongly marked difference between the two groups. Only a few are completely passive (rocking), while in the active ones the body is sometimes subjected to a passive motion for a long period of time (skiing).

§1. *Passive Games Involving the Static Organ.*

The most characteristic group is that of the passive games, since they are based on specific sensations of the organ involved. The important role of the static organ is most distinct, and their particular influence on the mood of the player prevents them from being comparable with others. In fact, the latter fact constitutes the motive for the game. /146

It is worth noting that despite this, the importance of the organ for our consciousness has been considerably underestimated. This may be because it is not easy to describe these sensations, since they are less strong and have a more general type of influence on the psyche. Purkyne [55] describes these sensations for swinging, as follows:

"A feeling of calmness, slow breathing (a consequence of loss of blood from the upper regions toward the feet), a pleasant feeling in the internal organs and in the lower part of the body. This is at the beginning. The feeling continues to rise from the lower part of the body toward the stomach, and turns into nausea; the head, too, is overcome by the same feeling to an ever-increasing extent by the same feeling which accompanies the nausea."

He does not mention the static sensation itself. It is our intention to begin with precisely these principles in our dissertation.

At first glance, the idea of a general use of playful influences on the labyrinth strikes us as being rather surprising. Everyone who serves as a subject in studies of labyrinth function soon notices that all his observations are accompanied by an unpleasant feeling. Blurring of vision, after-sensations, occasionally the production of an illusion, uncertainty regarding the real type of motion of his body, all of these lead to negative effects. All of these unpleasant feelings are combined most effectively in seasickness, as a result of the very strong and highly irregular stimulation of the labyrinth. /147

How is it now possible that such a completely different sensation is obtained in games? The blurring of the vision does not play a role in this because although this is one of the unpleasant aspects of the experiments, we noticed that people close their eyes in some of these games (swinging, rocking) in order to sense the pleasant sensations more purely.

Riding on the merry-go-round is an exception to this. This is an optical game; the low uniform velocity allows the labyrinth to remain at rest; only modern technology was able to involve the labyrinth by installing rocking boats and horses which imitate galloping. The optical illusion alone was apparently unsatisfactory.

The principle point must have been the manner in which the stimulus was produced. Every uniform acceleration, unless very small, is mostly unpleasant in its effects on the semicircular canals and the otoliths. In these games, the accompanying symptoms (loss of blood from the brain, upset stomach, residual dizziness) appear only after a long time in less sensitive persons. The acceleration is not uniform in any of the games. On the contrary, the latter is continually increasing and decreasing.

If we check with the games mentioned above to determine the extent to which this statement is true, we see that swinging in all its forms, rocking, and horseback riding (galloping) appear to affirm the idea completely. This is noticed particularly on the merry-go-round horses in which an eccentric mechanism has been installed to produce a steadily increasing and decreasing acceleration rather than the uniform acceleration which was boring.

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§2. Active Games Involving the Static Organ.

In the active games, the decrease and increase of acceleration is more noticeable in the motions of the muscles than in the movements of the labyrinth, which are small. Some of these games completely lack decrease and increase of acceleration, such as jumping and sliding from a height, skiing, stilt walking, and walking-the-beam.

In many of them, there is a second peculiarity which may be more important: in order to produce a supposedly pleasant effect, the game must be performed rhythmically.

The decrease and increase in acceleration mentioned above occur within the periods of that rhythm. The rhythm is completely regular in swinging, rocking see-sawing, horseback riding, dancing and skating.

The required length of a period is closely related to the appearance of the after-sensation. If the gentle rocking motion turns into a motion involving rapidly decreasing and increasing acceleration, so that the conflict between the sensation and after sensation becomes violent, unpleasant secondary symptoms appear to disturb the game. In a swing, where the period is dependent on the length of the rope, this can be demonstrated directly. The ropes of a swing must be at least 3 m long; if they are shorter, the periods of the swing will be shorter as well so that the present feelings described by Purkyne are spoiled by the resulting conflict which also involves blurred visual impressions.

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The significance of the rhythm as an economical method of energy distribution make it understandable that rhythm is desirable in the sensations of an organ which regulates voluntary motion.

Rhythmic motions, and the involuntary ones as well (heartbeat, breathing), supply the maximum useful effect with minimum fatigue. In the rhythmic sensations of the static organ, the tendency to such motions is still further intensified. It is no wonder that especially in active games such as dancing and skating which do not show as strong a need for decreasing and increasing accelerations, rhythm controls the game. This can be related more graphically to rhythm if we consider the active games as variations of normal walking. The latter, too, is rhythmic and regulated by the labyrinth. We will not discuss the reasons why walking (flying, swimming) are rhythmic. One might object that the muscles themselves had a tendency toward rhythm and that there was therefore a special inclination on the part of the labyrinth toward rhythm, especially since it regulates this muscle motion.

However, this is not true for passive games, since there is no muscle movement involved. Even in the active games the muscles show a tendency toward rhythm on account of the resultant increased productivity, but in some cases this can be clearly separated from labyrinth rhythm. Every skater knows the difference between normal skating in a forward direction and so-called "overskating". In both, the muscle movement is rhythmic, but it is only in overskating that the labyrinth is strongly stimulated by the displacement of the effect of gravity to the left and right; it is only then that the typical psychic effect which is the object of the action appears. /150

If we examine this psychic effect in the different games further, we will note a still more significant difference between the two groups.

In the passive games, the motion produces a form of hypnosis, which can lead to sleep (as in rocking).

In the active ones, the game has an exciting effect. Excessive passive motions such as high jumping, riding on a roller coaster, etc., also have an exciting effect. This may be explained by the violence of the sensation, the difficulty in achieving equilibrium, the stimulation of the danger, and other secondary factors.

In general we can say that rhythmic oscillating labyrinth stimulation has an anesthetic or exciting effect depending on whether it leads to purely static sensations or to rhythmic motions.

We have already pointed out this contrast by using the concepts of passive and active games, but it is the particular task of the labyrinth itself to enforce both psychic conditions (hypnosis or narcosis, and excitation), regardless of the contrast

between them. As we noted in discussing the passive games, the labyrinth has a direct action through the sensations it produces, while in the active games it acts more indirectly through its reflexes. In both actions, the labyrinth relies on the related auditory organ. /151

The two attributes of these stimuli which cause pleasant sensations are found in the art of music.

Yet even in this respect the two organs developed from the same structure play a role analogous to that of no other organ.

In music, the increase and decrease of the stimulus is represented by crescendo and decrescendo; of course, rhythm forms a basis of all music.

This seems a rather far-fetched comparison; it is true that the auditory organ, being so much more developed, should not be equated with the primitive labyrinth in view of its incalculable versatility. Nevertheless, the fact that the stimuli from the two organs work so well together proves to us that this similarity is not exaggerated but is actually based on the nature of the two organs.

In rocking (in a cradle or in the arms), we have the lullaby, and in dancing there is the dance music which supports the rhythm; in the first case, this is used as a subject and object of the action. In addition, in both cases the increasing and decreasing of the motion is accompanied by crescendo and decrescendo.

Dancing then becomes the most complete expression of the two organs in their entirety. With this step, the action of the labyrinth moves from that of a game to that of an art. Here too, the psychic effect is also maximum. The nature of the accompanying music reproduces in a more subtle form the frame of mind produced by the labyrinth.

If we summarize the ideas mentioned above, we will find the following points: /152

1. The motion games derive their name from the fact that a stimulus is exerted on the labyrinth; in the passive ones, the sensations are the objects of the stimulation, while it is primarily the reflexes which are stimulated in active games.

2. The sensation is pleasant when it slowly increases and decreases within strictly regular periods. The same is true of the reflexes.

3. Passive stimulation has an anesthetic effect, while the arousing of reflexes supported by arbitrary motions has an exciting effect.

4. In music, we find an analogous function of the auditory organ, where the stimulus has the same attributes and can be readily compared in its effects with those mentioned above.

5. Since no other organ shows any character resembling this, we can interpret it as an affinity between the static and acoustic organs.

THESES

I

In rotation, the velocity of the motion in the head reflex of the frog is proportional to the intensity of the stimulus.

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II

Two opposite rotation stimuli can eliminate the effects of one another before a sensation is produced.

III

The sensation of rotation increases less intensely before its maximum then immediately after its origin.

IV

In a classification of games according to the organs involved, a category of "games of the static organ" should be included.

V

In their functions, the static and acoustic organs give definite evidence of their phylogenetic affinity.

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VI

Congenital defects in the canalis Schlemmii have a very important relationship to the etiology of the buphthalmus.

VII

The visual disturbances produced by loss of blood are caused by changes in the optic nerve involving inflammation.

VIII

The taste buds of the tongue have fibers which lead through the tympanic cavity and reach the center through the glossopharyngeal nerve. A small portion follows the superior laryngeal nerve and the vagus nerve.

A vertically situated, siphon-shaped stomach is normal in adults.

X

The diet of Voit is too high with respect to albumen.

XI

Infection of the gall bladder during typhus abdominalis has a descending path.

XII

Acute anterior poliomyelitis and epidemic cerebral spinal meningitis are related in illnesses.

XIII

Lumbar stovaine anesthesia should be considered only when there are definite objections against other forms of anesthesia.

XIV

Dysmennorrhoea membranacea differs only in degree from normal menstruation.

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